EFFECTS OF HYPERABUNDANT MOOSE (*Alces alces*) ON STREAM ECOSYSTEM FUNCTIONING AND STRUCTURE IN CAPE BRETON HIGHLANDS, NOVA SCOTIA

by

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ABSTRACT

Terrestrial consumers can influence forest regeneration, but few studies have investigated the impacts of terrestrial consumers on freshwater ecosystems. I investigated the potential for cross-ecosystem effects of hyperabundant moose on stream ecosystems in the Cape Breton Highlands, Nova Scotia. I predicted that watersheds with higher moose impacts would have higher stream temperatures, total nitrogen, electrical conductivity, periphyton biomass, and macroinvertebrate abundances. I analyzed existing long-term data on 3rd and 4th order streams and conducted a field study on 1st and 2nd order streams to test for cross-ecosystem impacts of moose in the Cape Breton Highlands. I found evidence for moose impacts on total nitrogen and electrical conductivity. However, I found no evidence for higher stream temperatures and periphyton biomass, with limited evidence of moose impacts on macroinvertebrate abundances. This study provides insight into the effects of large ungulates within and across boreal forest ecosystems with potential implications for landscape-scale management of hyperabundant ungulates.

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

CHAPTER 1: Introduction

1.1 Herbivores as agents of disturbance

Consumers play a fundamental role in altering the dynamics and productivity of ecosystems (Leroux and Loreau 2010; Schmitz et al. 2010) and consumer effects can often cascade to influence the abundance and productivity of lower trophic levels (Carpenter et al. 1985). Through selective foraging, herbivores can influence plant community structure by altering plant biomass and growth rates and the flow of nutrients (Pastor and Naiman 1992; Leriche et al. 2001). Grazers and browsers seek out nutrient and mineral rich plant species for consumption, however, evidence shows different consequences of grazing versus browsing for plant communities. Specifically, grazers can enhance nitrogen availability in target plant species (Ruess and McNaughton 1984) and support highly productive patches with higher nutritional content relative to un-grazed patches (McNaughton 1983). For example, wildebeest grazing has been shown to enhance plant growth and diversity in areas of the Serengeti National Park in Tanzania (McNaughton 1983). Conversely, browsing tends to decrease nitrogen availability in soils (but see Ellis & Leroux 2017) resulting in shifts in plant community structure to more spruce dominated stands in boreal forests (Pastor et al. 1988; McInnes et al. 1992; Pastor and Cohen 1997). For instance, on Isle Royale National Park moose prefer to browse white birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), and balsam fir (*Abies balsamea*) thereby lowering litter quantity and quality, affecting nutrient cycles and soil fertility (McInnes et al. 1992; Pastor and Naiman 1992; Pastor et al. 1993). In my

thesis, I will focus on browsing herbivores (*i.e.* moose) and their far-reaching capacity to influence the boreal forest ecosystem.

Selective foraging by moose can have profound repercussions on the integrity of the forest (Pastor et al. 1988), especially when coupled with other disturbances. Insect disturbances are a common feature of boreal forests of eastern Canada, with spruce budworm (*Choristoneura fumiferana*) outbreaks causing severe defoliation in balsam fir stands periodically throughout the region (Kettela 1983). Between 1974 and 1984, Cape Breton Island, Nova Scotia endured a large-scale spruce-budworm outbreak that killed ~90% of the mature balsam fir trees (Ostaff and MacLean 1989). After this outbreak, models predicted the forest to be initially dominated by white birch and mountain ash (*Sorbus americana*), with eventual return to balsam fir dominant stands (Smith 1998). Past studies have shown the ability of fir-spruce stands to quickly regenerate after released from insect disturbance ensuring the stability of the system (MacLean 1984, 1988). However, moose over-browsed hardwood saplings and young balsam fir in the budworm affected areas (Basquill and Thompson 1997), thus altering the direction of forest regeneration and creating vast areas of spruce-moose savannah – particularly in Cape Breton Highlands National Park (CBHNP) (Smith 2007). In addition to increased browsing opportunities, Cape Breton Island moose have no natural predators and very little disease which further facilitated the moose population to reach hyperabundance (2 moose/km^2; Parks Canada 2015).

These alternate forest successional pathways are not only observed in Cape Breton Highlands National Park, Nova Scotia, but also in other areas of moose hyperabundance

such as Isle Royale National Park in Michigan, USA and the island of Newfoundland, Canada. Here we see similar scenarios of low levels of predation coupled with abundant food sources allowing populations to increase beyond normal thresholds thereby impeding forest regeneration. For instance, the 1980s collapse of the wolf population on Isle Royale allowed moose to increase substantially leading to severe over-browsing of balsam fir (McLaren and Peterson 1994). High abundance of moose in this area have been gradually converting forests into spruce-moose savannas (Pastor et al. 1988); however, when wolf populations increased due to reduced inbreeding, balsam fir were released from the pressure of intense moose herbivory and grew into the canopy of the forest (Vucetich and Peterson 2014). In Newfoundland, the scenario is comparable to Cape Breton Island where wolves have long been extirpated (Pimlott 1953) and predation is limited to hunters and black bears (*Ursus americanus*) preying on young calves (McLaren et al. 2009). The impacts of moose are so great on the island of Newfoundland, that Parks Canada has implemented moose hunting as an active restoration technique in Gros Morne and Terra Nova National Park in 2011 (Tom Knight, Project Manager II, Parks Canada *personal communication*). CBHNP followed suite with a similar restoration approach beginning in 2015 (Clayton D'Orsay, Resource Conservation Officer II, Parks Canada *personal communication*). These examples of environments void of major natural predators clearly demonstrate the importance of food chain dynamics and the potential ecosystem impacts of hyperabundant consumers.

1.2 Trophic interactions across ecosystem boundaries

Meta-ecosystems are ecosystems connected by fluxes of energy, material and organisms influencing the links between landscapes (Polis et al. 1997; Loreau et al. 2003; Leroux

and Loreau 2008). For instance, riparian plant vegetation can contribute allochthonous energy and material (*i.e*. detritus) to adjacent headwater streams, influencing stream invertebrate and fish communities throughout the whole riverine ecosystem (Hynes 1975; Vannote et al. 1980). Similarly, terrestrial invertebrates make up a considerable portion of fish diets, influencing their distribution and population dynamics (Nakano and Murakami 2001; Baxter et al. 2005). Likewise, aquatic insect emergence contributes significantly to the diets and dynamics of terrestrial predators such as birds and spiders (Iwata et al. 2003; Henschel et al. 2001). Recent meta-analyses highlight the important direct and indirect effects of subsidies (*e.g.* nutrient, detritus, and prey) on a large number of ecosystems (Marczak et al. 2007; Allen and Wesner 2016). In some cases, indirect effects of resource and consumer fluxes differ in that bottom-up (*e.g.* nutrient and detritus) effects elicit a stronger response than top-down (*e.g.* prey and predator) effects (Allen and Wesner 2016). These studies demonstrate how biotic interactions across ecosystems are in large part determined by the fluidity of aquatic-terrestrial boundaries and how prey subsidies can have surprising effects on consumer productivity.

Consumers play a key role in modifying and maintaining cross-ecosystem dynamics and habitat complexity (McCann et al. 2005; Moss 2015; Bakker et al. 2016). In southern Africa, hippopotamus (*Hippopotamus amphibius*) increase habitat heterogeneity in riverine ecosystems by creating deep pools and paths between channels (Naiman and Rogers 1997). In addition, recent research suggests hippos feeding in savannah grasslands and defecating in riverine ecosystems are supplying an essential source of nutrients for aquatic consumers (McCauley et al. 2015). In Yellowstone

National Park, USA, elk (*Cervus elaphus*) browsing on riparian vegetation widen channels and increase riverbank erosion (Beschta and Ripple 2006; Beschta and Ripple 2008). Moose also facilitate the reciprocal flow of nutrients between freshwater and terrestrial ecosystems; their foraging on aquatic macrophytes, moose can transfer large amounts of nutrients to terrestrial environments via feces (Bump et al. 2009). Moose feeding in lakes can also increase nutrient releases in these aquatic ecosystems (Bump et al. 2017). Similarly, evidence shows moose directly altered riparian shrub communities and increased above ground nitrogen via faecal deposition (Butler and Kielland 2008). These studies highlight the tremendous influence that large herbivores have on the land-water interface and the potential to alter aquatic ecosystems in numerous ways (see reviews in Moss 2015; Bakker et al. 2016).

In areas of the Cape Breton Highlands, moose are responsible for stalling boreal forest regeneration and allowing for the advancement of grasses (*e.g. Calamagrostis canadensis*) (Smith 2007). The high densities of moose and subsequent changes to plant communities has major repercussions on wildlife. For instance, species diversity of songbirds at moose-mediated grassland sites was found to be lower than forested sites and abundance was low for all bird species monitored (Lauren et al. 2014). Similarly, it is possible that both terrestrial and aquatic invertebrate prey in these areas are being affected by moose-mediated changes in plant community regeneration. Furthermore, it is conceivable that loss of forest due to intensive ungulate herbivory could alter physical and chemical properties in adjacent aquatic ecosystems.

1.3 Effects of forest removal on stream ecosystems

The health of riverine ecosystems is directly tied to the health of the surrounding landscape with the riparian zone moderating all ecosystem processes (Hynes 1975; Gregory et al. 1991). Geomorphic, hydrological, and biological processes are all moderated within the corridor between land and water (Swanson et al. 1988), thus, changes to the landscape can directly affect the structure and functioning of stream ecosystems. The major stream issues related to forest removal outlined in this thesis deal with physical (stream temperature), chemical (nutrients and dissolved solids), and biological (periphyton and macroinvertebrates) attributes traditionally used to describe stream ecosystem health.

The removal of riparian and upland forests can increase stream temperatures (Jonson and Jones 2000; Gomi et al. 2006; Pollock et al. 2009). This increase has largely been attributed to increases in heat inputs via direct solar radiation (Beschta et al. 1987). However, research shows that increases in stream temperature are possible even with using 15-20 m wide riparian buffers (MacDonald et al. 2003; Jones et al. 2006). Therefore, the health of the entire forested watershed can impact stream temperature. For instance, Brosofske et al. (1997) discovered that upland forest removal contributed to increases in stream temperature by the heating of soils containing shallow ground-water aquifers throughout small streams in western Washington, USA. Thus, streams flowing through areas subject to intense moose herbivory may have degraded riparian buffer zones with subsequent indirect effects on stream temperature dynamics.

The loss of treed biomass can alter biogeochemical processes, thus altering stream water chemistry. For instance, nutrient uptake by forests can limit overland flow by storing nutrients within their tissues (Keenan and van Dijk 2010). The loss of biomass allows nutrients to be released after forest harvesting, with many studies showing the removal of riparian buffers can increase total nitrogen in streams (Richardson and Beraud 2014). To avoid surface runoff after forest removal, riparian buffers can successfully limit increased nitrogen inputs. However, riparian buffers comprised of forests that are >50 m wide are more effective at reducing nitrogen inputs to nearby streams than small (0-25 m) grassland buffer strips (Mayer et al. 2007). Changes in plant communities can also affect nitrogen inputs in streams, namely the appearance of nitrogen-fixing alders. Alders are pioneer species that readily grow in disturbed landscapes after forest felling due to exposed mineral soil and high solar radiation (Wipfli et al. 2003). Moose typically avoid browsing the unpalatable alder species due to its chemical defence strategies (Hollingsworth et al. 2010). In lieu of no empirical evidence on this topic I expect, the removal of treed vegetation and shifts in riparian plant communities as a result of moose may exert similar effects on total nitrogen in streams.

Electrical conductivity is another water quality parameter often used to determine effects of forest removal on adjacent stream ecosystems. Electrical conductivity measures the amount of dissolved ions such as Ca^{2+}, Mg^{2+}, and Na^{+} found in stream water (Welch et al. 1998). Forest removal accelerates surface runoff and soil erosion which allows dissolved solids to reach neighboring environments more readily (Foster and Bhatti 2006). For instance, the loss of treed biomass reduces rainfall interception by the canopy,

as well as evapotranspiration that allows for higher water yields which can be exasperated on steep landscapes due to accelerated erosion (Hamilton 2008). Research shows elevated levels of electrical conductivity after forest clearing, even several years after harvesting occurred (Reuss et al. 1997; Richardson and Beraud 2014). Additionally, recent research looking at hydrogeochemical responses after bark beetle disturbances discovered increased electrical conductivity in streams over a seven-year period (Su et al. 2017). Therefore, the reduction of forest canopy cover and increase in degraded forested habitat due to hyperabundant moose could influence the amount of dissolved solids entering nearby streams.

In addition to altered stream temperature and water quality, forest removal can cause changes in stream biota. Studies have shown algae communities or periphyton biomass increased in streams sampled after forest harvesting (Murphy et al. 1981; Kiffney et al. 2003). This was largely attributed to increased solar radiation due to lack of shading in open reaches of logged streams, however, nutrient influxes and trophic structure of invertebrates also could have been contributing factors (Kiffney et al. 2003). Changes in periphyton abundances shift the energy base often causing changes in macroinvertebrate assemblages. For instance, higher autochthonous production in streams subject to forest clearing tend to increase grazing invertebrate abundance while decreasing the abundance of shredding invertebrates (Bilby and Bisson 1992; Stone and Wallace 1998). Additional changes in community structure also follow changes in the energy base such as increases in collector-gatherer and predatory invertebrates (Murphy and Hall 1981; Hawkins et al. 1982; Kedzierski and Smock 2001). While filter-feeding

invertebrates tend to decrease directly after forest felling, then rebound several years later possibly due to elevated nutrient levels (Haefner and Wallance 1981). These changes in macroinvertebrate community structure often lead to general increases in total abundances and EPT abundances (Newbold et al. 1980; Murphy and Hall 1981; Stone and Wallace 1998; Kreutzweiser et al. 2010; Jackson et al. 2007). Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies) form the metric EPT, commonly used as a bioindicator of stream quality. Overall, changes in incidental light levels in stream reaches subject to intense moose herbivory could possibly influence algae growth thereby altering macroinvertebrate community structure and abundances.

Although, moose altered landscapes are different from forest harvested landscapes, the above literature offers insight into how aquatic systems may be adversely impacted by moose. As discussed previously, browsing herbivores can influence forest regeneration by decreasing the amount of palatable plant species thus changing the dominant plant species to less palatable, lower quality species (high carbon: nitrogen) (Pastor et al. 1988). This may be different from forest harvesting scenarios in which clear-cutting removes all trees in a given section, leaving behind only a few stands. Also, soil erosion is a major problem during clear-cuts (Croke et al. 1999) with surface runoff having a higher magnitude than would be expected in the removal of targeted plant species by moose. Despite these differences following insect disturbance, the conversion of forest into grassland by hyperabundant moose is a continued disturbance to the ecosystem, while clear-cutting scenarios allow for regeneration post-disturbance. Thus,

lack of forest recovery can still influence adjacent ecosystems in similar ways to canopy cover removal.

1.4 Thesis Objectives, Structure, and Significance

As discussed, intense moose browsing can influence forest regeneration by first stunting trees which after repeated browsing die thereby transforming vast areas of forest into spruce-moose savannah (Pastor et al. 1988, Smith et al. 2010). Here I propose that moose-mediated grasslands can influence adjacent stream ecosystems in a variety of ways. For instance, moose create more open riparian zones that will likely lead to streams more exposed to sunlight and higher water temperature. The decline in forest may cause less rainfall interception by forest canopy resulting in more overland flow and transport of dissolved nutrients. These direct effects of hyperabundant moose can cascade to influence streams indirectly by altering the amount of periphyton biomass and macroinvertebrate assemblages. Therefore, the primary objectives of my research were to determine the effects of hyperabundant moose on stream functioning and structure by looking at changes in stream temperature, nutrients, and stream biota.

In order to evaluate the effects of hyperabundant moose on stream ecosystems, I conducted a multiscale investigation in Cape Breton Highlands, Nova Scotia. In Chapter 2, I analyzed long-term stream temperature, water quality, and macroinvertebrate data on 3rd and 4th order streams found throughout various regions of Cape Breton Highlands National Park in relation to moose impacted landscape. In Chapter 3, I designed a field study in order to examine the effects of moose impacted landscapes on 1st and 2nd streams in Cape Breton Highlands. I compared stream temperature, total nitrogen, electrical

conductivity, periphyton biomass, and macroinvertebrate community structure data for 14 streams along a gradient of moose impact (*i.e.* 0 – 69% moose-mediated grasslands in watershed).

To my knowledge, this is the first study investigating the effects of hyperabundant moose on stream ecosystem structure and functioning, offering insight into cascading impacts of large terrestrial consumers across ecosystem boundaries. Specifically, this empirical work contributes to the development of meta-ecosystem theory by filling an important gap in our understanding of cross-ecosystem fluxes. This information may prove useful for other areas experiencing effects of hyperabundant moose, such as Terra Nova National Park in Newfoundland or Isle Royal National Park in Michigan. Furthermore, information contained in this thesis provides guidance to water resource managers in the event of another severe spruce budworm outbreak in the boreal forest region.

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CHAPTER 2: Watershed-scale effects of hyperabundant moose on stream ecosystems

2.1 Introduction

Moose (*Alces alces*) are drivers of change in the boreal forest by altering plant communities, energy flows and nutrient cycling with selective foraging (Pastor and Naiman 1992). Selective herbivory by browsers can have both direct and indirect effects on terrestrial ecosystems. For instance, moose browsing alters plant species composition to more spruce-dominated forests, thereby affecting nutrient cycles and soil fertility (Pastor et al. 1993, Kielland and Bryant 1998, Persson et al. 2005). High densities of moose can severely impact boreal forests through repeated browsing of balsam fir (*Abies balsamea*) and white birch (*Betula papyrifera*) saplings, stalling regeneration after insect disturbances (Smith 2007). Lack of regeneration due to hyperabundant moose has transformed areas of the boreal forest of Cape Breton Highlands National Park (CBHNP) into open and grassland dominated landscapes. While there exists a good understanding of moose impacts on terrestrial ecosystems, few studies have investigated the cross-ecosystem effects of moose on freshwater ecosystems (Bump et al. 2009, Bakker et al. 2016, Bump et al. 2017). This chapter seeks to fill this gap by investigating the effects of hyperabundant moose browsing in watersheds on stream ecosystem function and structure.

Moose over-browsing and the subsequent formation of grasslands can impact aquatic ecosystems in numerous ways. For instance, intensive moose herbivory should create more open riparian zones that will likely lead to streams being more exposed to

sunlight, producing higher water temperatures. Similar higher temperatures were recorded for streams with removed riparian vegetation resulting from forest harvesting (Johnson and Jones 2000, Gomi et al. 2006). Increasing stream temperatures are not exclusive to riparian zone tree removal, but also basin-level harvesting with adequate buffer zones. Pollock et al. (2009) determined that average daily maximum stream temperatures were correlated to total basin harvested, while MacDonald et al. (2003) showed elevated stream temperatures even with 20m buffers in place. These studies highlight the additional pathways of altering temperature regimes, not only from the removal of riparian vegetation, but also upland vegetation of streams with shallow ground-water sources (Pollock et al. 2009).

The removal of the forest canopy can also affect the amount of nutrients and total dissolved solids entering the stream. Watersheds with higher amounts of grassland may have less rainfall interception by forest canopy resulting in more overland flow and transport of dissolved nutrients. Richardson and Beraud (2014) conducted a global synthesis that reported higher levels of total nitrogen and electrical conductivity in streams where the riparian buffers were removed during commercial forest harvesting. In spruce-hemlock forests removal of riparian vegetation causes increases in nitrogen-fixing plant species, such as red alder (*Alnus rubra*), thereby increasing nitrogen in streams (Wipfli and Musslewhite 2004). While total nitrogen can be related to specific changes in plant communities, conductivity is a useful indicator of changes in dissolved ion concentrations, and can be used as a surrogate for additional nutrients indicating further chemical analysis is required (Gali et al. 2012).

As well as increasing stream temperature and nutrients, loss of riparian canopy can alter macroinvertebrate community structure. Several studies have demonstrated substantially higher levels of all functional groups after forest removal (Newbold et al. 1980, Stone and Wallace 1998, Fuchs et al. 2003), with some reporting elevated levels of EPT (Ephemeroptera, Plecoptera, and Trichoptera) invertebrates (Jackson et al. 2007). In some cases, elevated total abundances are detected years after forest harvesting. For instance, Stone and Wallace (1998) found invertebrate abundance was higher even 16 years after the clear-cut disturbance nearby mountain streams of Mason County, North Carolina, likely due to increased nutrient availably. Additionally, shifts in macroinvertebrate community structure due to increased solar radiation causing greater autochthonous production after forest harvesting can increase abundances of grazers, collector-gatherers, and predatory invertebrates (Murphy and Hall 1981, Hawkins et al. 1982, Kedzierski and Smock 2001). Likewise, the removal or reduction in riparian vegetation among streams decreases allochthonous inputs, specifically altering the quality of organic matter and suspended particulate material, thereby impacting macroinvertebrates such as shredders and filter-feeders (Haefner and Wallace 1981, Stone and Wallace 1998).

The major impacts of forest removal on stream temperature, water chemistry, and macroinvertebrate assemblages show the importance of riparian vegetation to stream ecosystem functioning and structure. Although, moose over-browsing effects may be less pronounced than forest harvesting effects (see Chapter 1 section 1.3), a full understanding of changes to aquatic ecosystem structure is essential to understand and mitigate any

detrimental effects of moose browsing on stream ecosystems. Therefore, my study aims to test the following predictions:

a) streams in watersheds with higher levels of moose impacted landscapes will have higher stream temperatures;
b) streams in watersheds with higher levels of moose impacted landscapes will have higher total nitrogen and electrical conductivity;
c) streams in watersheds with higher levels of moose impacted landscapes will have higher total and EPT (Ephemeroptera, Plecoptera, Trichoptera) abundances, as well as altered macroinvertebrate community structure. with more grazers, collector-gatherers, and predatory invertebrates present. Shredding and filter-feeding invertebrates will be lower in grassland streams than forested streams.

2.2 Methods

Study Area

I conducted my study in Cape Breton Highlands National Park (CBHNP), located in the northern region of Cape Breton Island, Nova Scotia, Canada (see Figures 2.1 and 2.2). The temperate maritime climate is largely governed by the Gulf of St. Lawrence and the Atlantic Ocean which surround the island. Cape Breton Highlands is part of the Acadian Forest Ecozone and can be divided into several distinct groups: Acadian (mixed hardwoods and softwoods), Boreal (fir, spruce, and birch), and Taiga (boggy wetlands and barrens) (Neily et al. 2003). The boreal forest region is primarily located on the

south-central and western highland plateau of CBHNP. Weather on the plateau is notably different than lower-lying regions, with rapid changes in temperature, as well as rain and snowfall. This is because the plateau is approximately 400 meters above sea level, making for abundant snowfall that stays late into the season (Neily et al. 2003).

The Acadian forest region is found in river valleys and coastal lowlands, characterized by sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia*) eastern hemlock (*Tsuga canadensis*), and balsam fir (Parks Canada 2009). The plateau of the boreal forest region is characterized by balsam fir, as well as black spruce (*Picea mariana*), white spruce (*Picea glauca*) and white birch (Parks Canada 2009). The Taiga forest region is likewise located on top of the plateau and is characterized by barren landscape with stunted softwoods and boggy wetlands. Black spruce, balsam fir, tamarack (*Larix laricina*) dominate the region with sphagnum moss in open bogs and reindeer lichens making up the drier barren landscape (Parks Canada 2009).

The geology of the highland plateau is largely metamorphic and igneous bedrock from the Late Precambrian to Middle Palezoic period, covered by a thin, discontinuous veneer of till and residuum (Baechler and Boehner 2014). Conversely, the lowlands and underlying floor of the canyons are comprised of sedimentary bedrock overlain by glacial till with intervals of colluvium and alluvial deposits of sand and gravel (Baechler and Boehner 2014).

Site Selection

Parks Canada has been periodically monitoring water quality and macroinvertebrates in representative study streams since 2005. These streams are found in various regions throughout the park and have been predominantly monitored using the standardized Canadian Aquatic Biomonitoring Network (CABIN) protocols (Environment Canada 2012). I obtained CABIN data for 40 sites chosen from the four water districts in the park: Central Highlands, Atlantic Slope, Atlantic Coast, and Gulf Coast (ELC 1978). The majority of these streams are considered mid-order (ranking 3rd and 4th order). The monitoring program was initially established to assess the overall reference condition of streams within the Park, as well as to examine the effects of various disturbances (*e.g.* dams, landfills, salt sheds, bridge) on streams. The nine sites monitoring these local disturbances were not used in the analysis, as well as five sites that exceeded the set limit of >1 km^2 and < 65 km^2 and two sites that were sampled late in the season were dropped from the analysis (Appendix Table A1). In addition, three watersheds were dropped because they overlapped one another, in this case the site that was sampled repeatedly was retained for analysis. Thus, I retained 21 sites for water quality (total nitrogen and conductivity) and macroinvertebrate analysis that were sampled during the fall of 2005-2014 (see Appendix Table A1 for summary of sites; Figure 2.2). For stream temperature, not all the above CABIN sites have been monitored; therefore, 12 sites were selected based on suitability for the above set limitations (see Appendix Table A1; Figure 2.1).

Grasslands and open areas as a proxy for moose impacts

In the highlands of Cape Breton, moose herbivory has changed the structure of the forest ecosystem. Spruce budworm (*Choristoneura fumiferana)* epidemics during the 1970s and 80s killed up to 90% of the mature balsam fir forest (Ostaff and MacLean 1989). The regenerating forest consisting of white birch and balsam fir provided an abundant food source for moose, which combined with low levels of predation and disease, allowed moose populations to reach hyperabundance. Moose browsing on the plateau of Cape Breton Highlands has altered the normal successional trajectory of this boreal ecosystem and led to sustained grass (*Calamagrostis* spp.) and open areas dominating the landscapes (Smith et al. 2010).

Impacted boreal forest was first classified using SPOT5 imagery from 2005 and aerial surveys resulting in four classes of disturbance: blown-down, browsed deciduous, grass, and snag (Smith 2007). A declining gradient of forest regeneration has been identified, with grassland having the lowest levels of regeneration and the highest levels of tree mortality (Smith 2007). Recently, SPOT5 imagery from 2013 was used by Parks Canada to improve classification of the deteriorated boreal forest creating the categories: grass, open/intolerant/bracken, and fern (Lemieux 2015). The data used in this study corresponds to the 2013 classification; however, on comparison much of the previous browsed deciduous and blown-down categories are have now transitioned to grass (Matthew Smith, Ecologist, Parks Canada, *personal communication*).

To assess moose impact at the landscape scale, I used percentage of non-forest (grass, open/intolerant/bracken, fern) as classified by the 2013 SPOT5 imagery analysis

in the watershed as a proxy for the degree of impairment in natural vegetation succession exerted by intense moose herbivory. I refer to these moose impacted sites as *grasslands* for the remainder of the chapter. To determine percentage of grassland at these sites, I delineated watersheds using SPOT5 land classification from 2013, digital elevation model (DEM) data, watercourses and site locations. I used surface hydrological modeling tools in ArcGIS™ Desktop 10.2.2, specifically fill, flow direction, and flow accumulation. The fill tool fills in sinks of the DEM thereby removing errors, flow direction determines the direction of water flowing from every cell, and flow accumulation calculates the accumulated flow of the cells that flow into each downslope cell (ESRI 2017). I then created pour points at the monitoring site defining the watershed as everything upstream from this point, and snapped it in place at highest flow accumulation. Lastly, I used the watershed tool inputting flow direction and pour points to delineate the watershed.

After the watersheds were successfully delineated for all monitoring sites and transformed into polygons, I intersected each watershed polygon with a land class polygon to calculate the percentage of grassland per watershed. The percentage of watershed designated as grassland was used as the proxy for moose browse intensity in the watershed.

Stream Temperature Data Collection

Continuous temperature was monitored hourly for the chosen sites throughout CBHNP using Hobo™ water temperature pro V2 data loggers. These loggers were placed in streams protected either with permanent housing or PVC constructed pipe housing as to limit direct solar radiation and anchored in place with rebar as outlined in the Water

Temperature Monitoring Protocol for CBHNP. The loggers were placed in the stream in late spring/early summer and retrieved in fall between the years 2005-2016. The 12 sites chosen had consistent data for the summer season (see Appendix Table A1), as some sites were removed from the analysis due to erroneous data (*e.g.* logger out of water, improper logger setting). Thus, June 21st to September 22nd was employed for summer stream temperature analysis. I calculated average and maximum stream temperature, as well as average daily maximum (ADM) stream temperature (maximum temperature averaged over the 89 days of the summer).

I expect natural variation in stream temperature to be driven by climate, riparian canopy cover, stream morphology, and groundwater influxes (Poole and Berman 2001). Consequently, I added data on air temperature, stream order, watershed area, and slope into my models to account for this natural variability. Groundwater and canopy cover measures were not accounted for in the model due to inadequate data. I determined watershed area from the watershed delineation, and stream order was obtained through the CABIN database provided by Parks Canada. To get an accurate measure of slope for the entire watershed, I used the clip tool in ArcMap to clip contour lines representing elevation and obtained the length of each line. I then used the following formula to obtain the average slope for the entire watershed: length of contour lines (m) x contour interval (m)/ watershed area (m^2). I acquired air temperature data for three weather stations throughout the study area (Ingonish Beach, Cheticamp, and North Mountain), and used the Environment Canada weather station data most geographically proximate to the study site (Government of Canada 2016). Air temperature data were inspected for errors and an

alternate weather station from Nova Scotia Department of Natural Resources (NSDNR) was referred to for missing North Mountain data in recent years. Daily mean, maximum, and minimum air temperatures were extracted from these data, while average daily maximum (ADM) air temperature was determined over the course of the summer from 2006-2016.

Total Nitrogen and Electrical Conductivity Data Collection

Water samples were collected once during macroinvertebrate sampling or in the fall season for 2005-2014, adhering to CABIN procedures (Environment Canada 2012). Approximately 500 ml of sample was taken for total nitrogen and specific conductance (temperature corrected electrical conductivity) analysis. Water samples were kept in a cooler and analyzed by the Atlantic Laboratory for Environmental Testing in Moncton, New Brunswick.

Total nitrogen and electrical conductivity values were obtained for the 21 sites from Parks Canada's water quality database. I expect natural variation of total nitrogen and electrical conductivity to be driven by stream order, riparian vegetation, underlying bedrock, slope, and groundwater inputs. While riparian vegetation offers insight into nutrient content, the lack of data on specific streamside vegetation types dictated this measure was not included in the models. Additionally, groundwater inputs and bedrock geology were not included due to lack of accessible data. The remaining environmental variables were determined as previously described for steam temperature, while elevation

was calculated as the mean basin elevation upstream from the sampling point to give a better indication of the overall effect of elevation.

Macroinvertebrate Data Collection

Macroinvertebrate sampling was conducted in the fall of 2005-2014 complying with CABIN protocols for wadable streams, where kick-netting is carried out for three minutes using a zigzag sampling pattern (Environment Canada 2012). Invertebrates were transferred to ethanol-filled jars and shipped for identification by CABIN certified taxonomists at Environment Canada. Macroinvertebrate and habitat data collected during CABIN sampling was obtained through Park's Information Centre on Ecosystems (ICE), a data storage and sharing system for Parks ecosystem science (Clayton D'Orsay, Resource Conservation Officer II, Parks Canada, *personal communication*). Macroinvertebrate data pertaining to the 21 sites were compiled and entered into the online CABIN database which contains different tools to determine if test sites are in reference condition and provides a variety of biological metrics used for stream assessments (Environment Canada 2016). I used the database to determine metrics pertaining to total abundance, EPT abundance, and functional feeding groups.

Macroinvertebrate community structure is controlled by a variety of physical and chemical parameters. To account for natural variation in invertebrate communities, the following physical characteristics were considered: stream order, watershed area, canopy cover ranking, elevation, and substrate. While canopy cover ranking gives insight into riparian vegetation inputs, an important contributor to variation in macroinvertebrate

assemblages (Vannote et al. 1980), this measure was not included in the analysis due to limited data throughout the entire stream network.

General Statistical Modelling Approach

I used general linear and generalized linear models to test my predictions. I used a model with only the intercept as a null model to ascertain if adding additional fixed effects (*e.g.* percentage of grassland) improved model fit relative to a model with only the intercept. I measured variance inflation factor (VIF) and removed multicollinear covariates (*i.e.* VIF > 3) from each model set. Watershed area was removed from all my analyses as it was correlated with stream order. I used Akaike Information Criterion corrected for small sample size (AIC_C) to determine the weight of evidence in support of an effect of moose on stream temperature, total nitrogen, conductivity, and macroinvertebrate metrics (total abundance, EPT abundance and functional feeding groups). I also present R^2 or deviance explained (D^2; for macroinvertebrate data) as an additional measure of model fit (Guisan and Zimmermann 2000). Models with pretending variables (sensu Anderson 2008) or uninformative parameters (sensu Arnold 2010) were removed from each model set.

Temperature Models: To test prediction a), I fit three general linear models with three different stream temperature metrics as my response; ADM stream temperature, average stream temperature, and maximum stream temperature models. I included percent grasslands, year, stream order, and air temperature as covariates in each model.

Total Nitrogen and Electrical Conductivity Models: To test prediction b), I fit two general linear models; one with total nitrogen as response and one with electrical conductivity as

response. I included percent grasslands, year, elevation, slope, and stream order as covariates in each model.

Macroinvertebrate Models: The invertebrate data exhibited over-dispersion; therefore, I used a generalized linear model with negative binomial distribution and a log-link for all invertebrate models. To test prediction c) I fit seven generalized linear models for total abundance, EPT abundance, and all functional feeding groups. I included percent grasslands, year, elevation, slope, stream order, and substrate size class (5: large pebble, 6: small cobble, 7: large cobble, 8: boulder, 9: bedrock) as covariates in each model.

2.3 Results

Moose effects on stream temperature

The percentage of grassland in the watersheds used for the stream temperature analysis ranged between 1 and 24 % (see Appendix Table A2), with an average of 10% (SD±6). I observed a negative relationship between grassland in the watershed and average daily maximum stream temperature (Figure 2.3). ADM stream temperature ranged from 10.5°C to 19.4°C, with the Grande Anse River being the coolest and Branch Pond stream the warmest (Appendix Table A2). Additionally, I observed a negative relationship between average and maximum stream temperature. Average stream temperature ranged from 10.1°C to 17.1°C, with Still Brook having the coolest and Fiset Brook having the warmest average stream temperature. Maximum stream temperature ranged from 16.9°C to 25.9°C, with Cheticamp River having the coolest and Branch Pond stream having the warmest maximum stream temperature.

The top model for ADM stream temperature included grassland, year, ADM air temperature, and stream order and explained 57% of the variation in ADM stream temperature for the monitored sites (Table 2.1). ADM air temperature and stream order were found to have a positive relationship with stream temperature. For average stream temperature, the top model included grassland and slope, explained 17 % of the variation in average stream temperature (Table 2.1). Slope was found to have a positive relationship with stream temperature. Finally, the top model for maximum stream temperature included grassland and maximum air temperature. This model explained 18 % of the variation in maximum stream temperature (Table 2.1).

Moose effects on Total Nitrogen and Electrical Conductivity

The percentage of grassland in the watersheds used for the total nitrogen and electrical conductivity analysis ranged from 1 to 50% (see Appendix Table A4), with a mean of 14 (SD± 11). I found a positive relationship between total nitrogen and grassland in the watershed (Figure 2.4). The range of total nitrogen was 0.06 to 0.49 mg/L, with the lowest value observed for Benjie's Brook and the highest value for McGregor Brook (Appendix Table A4).

The top model for total nitrogen included grassland, year of sampling, and stream order and this model explained 39% the variation in total nitrogen, while grassland alone explained 10% (Table 2.2). Stream order was found to have a negative relationship with total nitrogen in the sampled watersheds.

I also found a positive relationship between electrical conductivity and percentage grassland in the watersheds (Figure 2.4). Conductivity ranged from 26.2 to 163 µS/cm, with the lowest value recorded for Branch Pond stream and the highest for South Aspy River.

The top model for electrical conductivity included grassland, stream order, and elevation and this model explained 57% of the variation in conductivity for these watersheds (Table 2.2). I found grassland alone explained 40% of the variation in electrical conductivity (Table 2.2). The covariates stream order and elevation were found to have a negative relationship with conductivity in the sampled watersheds.

Moose effect on macroinvertebrates

The percentage of grassland in the watersheds used for the macroinvertebrate analysis was the same as for the total nitrogen and electrical conductivity analysis (see Appendix Table A5). The site Effie's Brook had the lowest total and EPT abundances recorded at 101 individuals and 87 individuals, respectively, both in 2007 (Appendix Table A5). While Warren's Brook at the highest total and EPT abundances recorded at 12,400 and 8,933 individuals, respectively, both in 2013 (Appendix Table A5). For functional feeding groups, shredder and grazer abundance was found to be lowest at Clyburn River in 2011 at 1 and 6%, respectively. While shredder and grazer abundance were found to be the highest at Branch Pond stream in 2008 and Effie's Brook in 2009, at 58 and 79%, respectively. For predators, Warren's Brook had the lowest abundance recorded in 2005 at 8% and the highest abundance at Clyburn River in 2011 at 90%. For filterers and gatherers, the lowest abundance was recorded

in Daphine's Brook in 2007 at 0 and 12 %, respectively. While the highest filterer and gatherer abundance was recorded at Warren's Brook in 2013 and Clyburn River in 2011, at 30 and 96 %, respectively (Appendix Table A5).

I found no evidence to suggest that higher percentages of grassland were related to higher numbers of invertebrates in the sampled watersheds. The top model for total macroinvertebrate abundance included grassland, year, stream order and substrate type and this model explained 42% of the variation in macroinvertebrate abundance (Table 2.3). This was largely due to variation between years, stream order, and differing substrate types (Table 2.3). Substrate type and stream order was found to have a negative relationship with total abundance (Appendix Table A9). In addition, I found no evidence to suggest that higher percentages of grassland were related to higher numbers of EPT macroinvertebrates. The top model for EPT macroinvertebrate abundance included grassland, year, stream order and substrate type, explaining 42% of the variation (Table 2.3) which was largely attributed to the environmental variables. Substrate type and stream order was found to exhibit a negative relationship with EPT abundance (Appendix Table A9).

Similarly, grassland explained little to no variation in functional feeding groups. (Table 2.3). The environmental variables year and stream order explained much of the 28% variation in shredder abundance, while year, stream order, and substrate explained much of the 44% variation in grazer abundance (Table 2.3). Stream order was found to exhibit a negative relationship with shredder abundance and a positive relationship with grazer abundance (Appendix Table A9). Additionally, substrate type was found to have a

positive relationship with grazers in the sampled watersheds. Likewise, to shredders and grazers, 37% of the variation in predator abundance was largely due to the additional variables year, stream order, and elevation. Stream order was found to have a positive relationship, while elevation was found to have a negative relationship with predators (Appendix Table A9).

For filterers and gatherers, I found evidence that grassland does explain some of the variation observed. Filter-feeding invertebrates had 27% of the variation explained by percentage grassland, as well as stream order, substrate, and elevation (Table 2.3, Figure 2.6); with grassland having a positive relationship with filterers, however explained only 0.3% of the variation (Table 2.3). Stream order, substrate type, and elevation were found to have a negative relationship with filter-feeders (Appendix Table A9). Gathering invertebrates had 51% of the variation explained by grassland, stream order, substrate, and elevation; grassland was found to exhibit a negative relationship with gatherers and explained 11% of the variation. (Table 2.3, Figure 2.6). Stream order, substrate type, and elevation were found to have a negative relationship with gatherers (Appendix Table A9). Yearly variation was found in most functional feeding groups, except for filter-feeders. Explanations of the findings pertaining to the year-to-year variation in functional feeding groups, as well as site comparisons are found in Appendix A.

2.4 Discussion

Moose densities have reached hyperabundance in Cape Breton Highlands National Park and mitigation efforts have been initiated to reduce terrestrial ecosystem impacts. However, aquatic ecosystems may also be impacted by moose over-browsing and

subsequent conversion of forest into grassland (Bakker et al. 2016). Heavy browsing occurs predominantly on the North Mountain plateau where two major river systems, the Grande Anse and North Aspy Rivers, originate. I found evidence of watershed-scale effects of moose on stream functioning with respect to nutrients, specifically at the Grande Anse and North Aspy River watershed sites.

Counter to my prediction, I found that stream temperature parameters were negatively related to percentage of grassland in the sampled watersheds (Figure 2.3). Previous studies investigating forest harvesting impacts on stream temperatures have found that the removal of riparian vegetation and upland vegetation increases stream temperatures (Johnson and Jones 2000, Pollock et al. 2009). But these studies usually measure smaller headwater streams (1^{st}-2^{nd} order) consistently over the monitoring period. For example, Johnson and Jones (2000) found elevated stream temperatures in headwater streams that were harvested over a period of 15 years. In the current study, I focused on mid-order reaches (3^{rd}-5^{th} order) that have much of the grasslands in the headwater region, having a large gradient between the headwaters and the mid-reaches of the monitoring sites. Therefore, any effect of moose could be weakened due to the surface water plummeting downhill to the lower reaches. Additionally, the sites with higher amounts of grasslands (Grande Anse and North Aspy River sites) were not annually sampled, while the sites with lower amounts of grassland were sampled ever year. Therefore, the lack of data for sites with higher amounts of grassland and the distance from the headwaters to the mid-reaches could counteract the warming effect that was predicted.

The watershed with the coolest water temperatures was the Grande Anse River. The Grande Anse headwaters originate on North Mountain, close to the North Mountain weather station. The air temperature recorded at the North Mountain weather station was 2°C cooler on average than the Cheticamp and Ingonish weather stations (see Appendix Table A3). As North Mountain is typically cooler and snow cover lasts on the plateau until late spring, it is unsurprising that headwaters originating here have cooler stream temperatures due to landscape and weather factors. Additional factors that were not included in the model, such as groundwater inputs may be influencing stream temperature as well. Although, groundwater data are limited in CBHNP, I can speculate what may be occurring. Roberts Brook, Corney Brook, and Clyburn River are all downstream from incised gorges and canyons allowing for more groundwater inflow (Fred Baechler, Chief Hydrogeologist, exp Services, *personal communication*). Therefore, I would expect these streams to have cooler summer temperatures due to groundwater influences (Chu et al. 2008), as is the case for Roberts Brook that also contains high levels of grasslands in the upper reaches. Therefore, the negative relationship between stream temperature and percentage grasslands may be indicative of factors not considered in the model. In addition, the size of the watershed may be influencing stream temperature regimes. Although, watershed area was found to be correlated with stream order, thus, higher stream temperatures are to be expected for larger tributaries.

In accordance with my prediction, I found total nitrogen to be positively related to grassland in the sampled watersheds. For total nitrogen, fewer trees and more open areas can reduce rainfall interception and facilitate greater surface runoff (Jakob and Hungr

2005). Nutrients once locked in biomass can be mobilized and an increase in soil nitrogen mineralization after forest removal allows for increases in stream nitrogen concentration (Mladenoff 1987, Holmes and Zak 1999). The magnitude of this response is dependent on soil properties and whether sufficient riparian vegetation was left in place (Lauren et al. 2005). Therefore, grassland and open areas are suspected to have higher total nitrogen mobilization (Mayer et al. 2007). However, grassland alone explained 10% of the variation, therefore, other variables should be considered as drivers that are not accessed in the model. For instance, riparian habitat surrounding streams, such as alders, can greatly influence nutrient concentrations. Alder is a nitrogen-fixing shrub typical of successional stages after timber harvesting (Moore and Richardson 2012). A shift to alder-dominated streamside vegetation could explain increased inputs of steam nitrogen during the fall season. In Chapter 3, I show evidence that higher levels of alders occur at grassland dominated streams in comparison to forest dominated streams.

Likewise, as predicted I found evidence to suggest electrical conductivity is positively related to grassland in the watersheds. Electrical conductivity or specific conductance measures the ability of water to carry an electrical current, and is greatly influenced by the amount of dissolved solids present (Artiola et al. 2004). Therefore, conductivity was used as a surrogate for ion burden in streams, suggesting surface runoff is more significant in grassland areas, or available ion-contributing materials are more available or subject to erosion in the watersheds at these locations (*i.e.* disturbed soils or reduced organic horizons exposing mineral layers) (Wenger 1984). Although, my conductivity model explained 57% of the variation, other factors such as underlying

geology and groundwater recharge were not included in the model and may also influence stream electrical conductivity. Both total nitrogen and electrical conductivity values measured in the present study are considered typical of pristine stream conditions. While this may be the case, responses of these water quality parameters to grasslands are consistent with studies conducted in forest harvesting settings (Reuss et al. 1997, Mayer et al. 2007, Richardson and Beraud 2014), and therefore offer insight into possible moose effects in these watersheds.

For total macroinvertebrate abundances and most functional feeding groups, there is little evidence to suggest that invertebrates are being affected by grassland habitat in the contributing watersheds. I predicted that overall macroinvertebrate abundance would increase, as would grazers, predators, and collector-gatherers, while stream shredders and filter-feeders would decrease in abundance with increasing moose impacts. However, there is no evidence to suggest increases in abundance, while very little to no evidence suggesting grazers, shredders, predators, and filterers are affected by grasslands. I did find evidence suggesting collector-gathering invertebrates had a negative relationship with higher percentages of grassland. This could be attributed to a decrease in fine particulate organic matter (FPOM), their main food source due to loss of riparian vegetation in the headwaters (Vannote et al. 1980). However, there appears to be no adverse response of other functional feeding groups leading to the conclusion that, in general, aquatic macroinvertebrates are only weakly impacted by grasslands sustained by intensive moose herbivory. More likely, macroinvertebrate community structure is strongly influenced by landscape and environmental variables (*i.e.* suitable substrate, stream order, year to year

weather-related variations) that may obscure watershed characteristics, including percentage grassland.

There is limited knowledge about the effects of moose on aquatic ecosystems, however, there is reason to suspect that they influence stream ecosystem function and structure based on other stressors (*i.e.* forest harvesting). Recently, studies have recognized the importance of moose on the aquatic-terrestrial interface (Bump et al. 2009, Bakker et al. 2016, Bump et al. 2017). However, their focus was largely on aquatic to terrestrial transfer of nutrients (Bump et al. 2009). Therefore, I provide the first study, to my knowledge, which examines the impacts of moose on aquatic ecosystems. As such, this study has several limitations due to the difficulty of studying a novel subject empirically. The water quality database provided by Parks Canada was extensive, however, the data were collected to give a comprehensive look at stream health for CBHNP and not designed to study the impacts of hyperabundant moose. Thus, data directly pertaining to the sites located on the moose disturbed plateau were not sampled extensively. Despite this, the models presented the best interpretations within these constraints, and do demonstrate relationships between water quality parameters and grassland in the watersheds of these streams.

In this study, I found evidence of moose effects on total nitrogen and conductivity. Stream temperature is governed by many landscape and environmental factors; therefore, the negative trend observed in these streams is debatable. Furthermore, large rivers included in this analysis are typically less affected by riparian shade and have more rapid heat conduction over a greater surface area (Poole and Berman 2001), therefore the

positive relationship between stream temperature and stream order is typical for larger systems that have overall large thermal inertia. Moose had little cross-ecosystem impacts on macroinvertebrate abundance and functional feeding groups. Thus, environmental and year-to-year variation influence macroinvertebrate community structure more than grassland in these watersheds (see Appendix A, Functional Feeding Group Composition). To improve understanding of moose effects on stream ecosystems, I conducted a field study on headwater streams on the moose disturbed plateau of North Mountain (Chapter 3). This will allow us to gain valuable insight into moose effects on stream ecosystems that may have been dampened in larger riverine systems.

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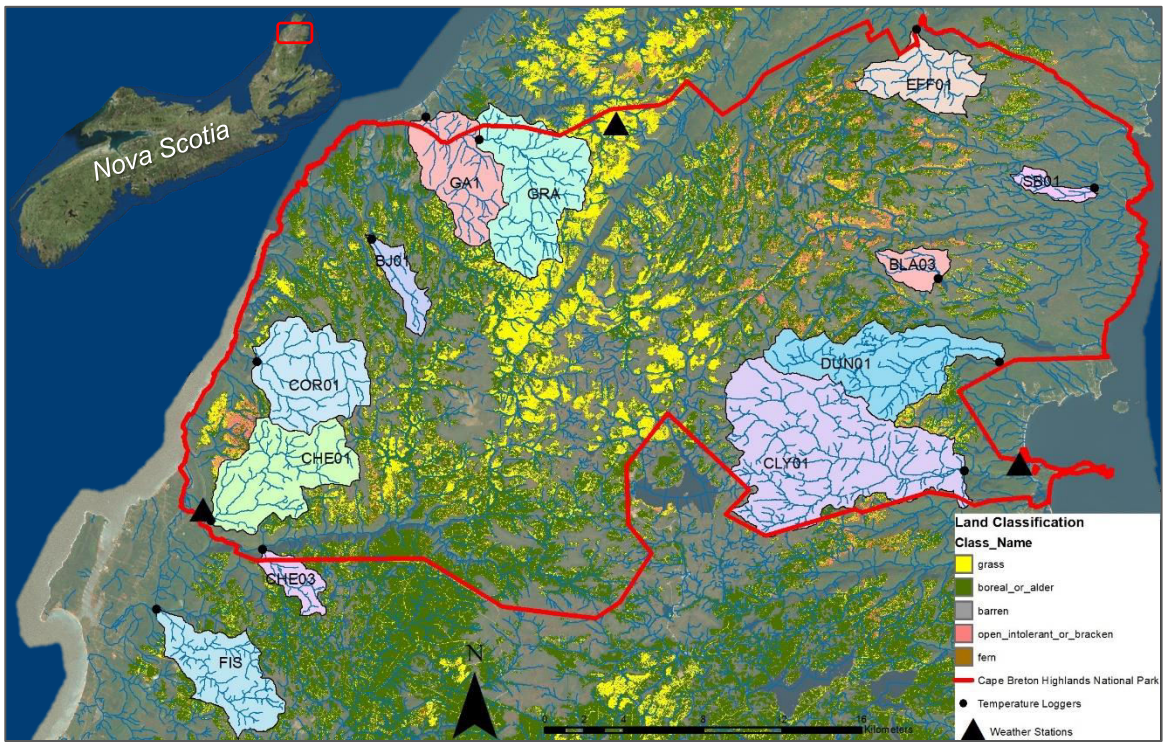

Figure 2.1: Watersheds included in the analysis for determining effects of grasslands on stream temperature in Cape Breton Highlands National Park. Base map source: ESRI; Data layer source: Parks Canada, 2013. Stream names: Benjie's Lake Brook (BJ01), Branch Pond Inflow (BLA03), Robert's Brook (CHE01), Daphine Brook (CHE03), Clyburn Brook (CLY01), Corney Brook (COR01), Dundas Brook (DUN01), Effie's Brook (EFF01), Fiset Brook (FIS), Grande Anse River (GA-1), Grande Anse River (GA), Still Brook (SB01). See Appendix Table A2 for percentage of grassland for each stream.

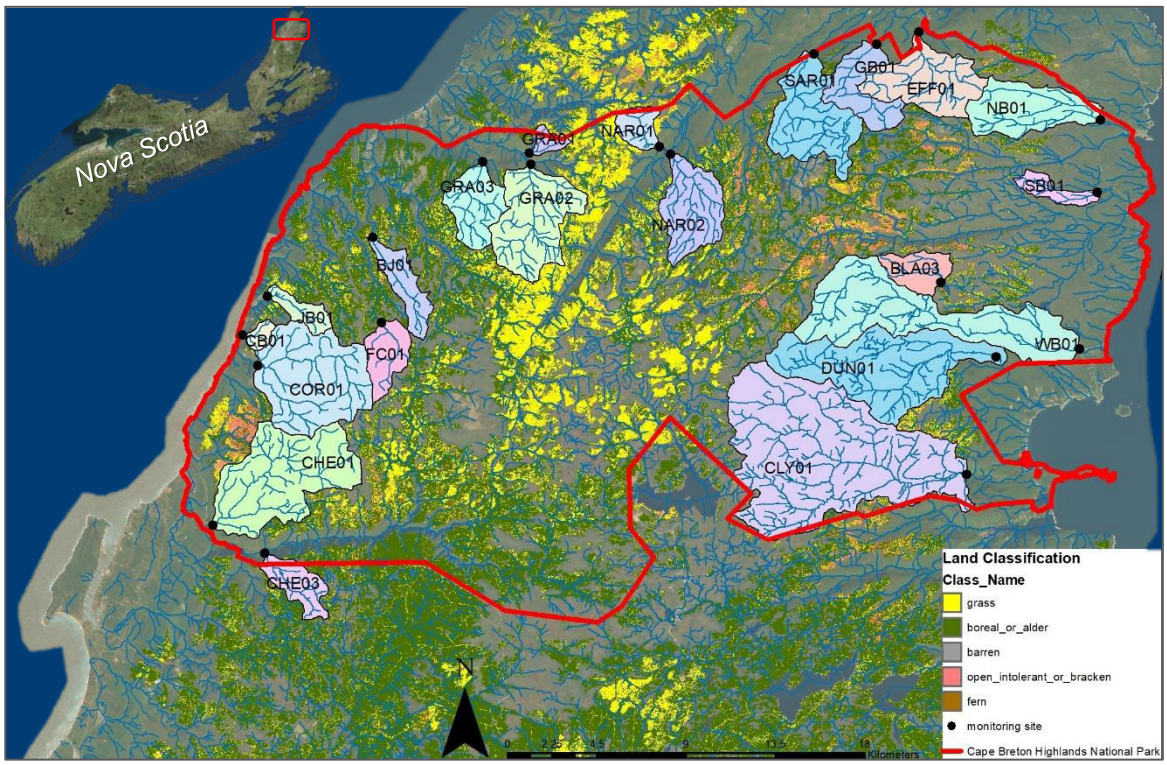

Figure 2.2: Watersheds included in the analysis for determining effects of grasslands on total nitrogen, conductivity, and macroinvertebrates in Cape Breton Highlands National Park. Base map source: ESRI; Data layer source: Parks Canada, 2013. Stream names: Benjie's Lake Brook (BJ01), Branch Pond Inflow (BLA03), Robert's Brook (CHE01), Daphine Brook (CHE03), Canadian Brook (CB01), Clyburn Brook (CLY01), Corney Brook (COR01), Dundas Brook (DUN01), Effie's Brook (EFF01), Fishing Cove River (FC01), Glasgow Brook (GB01), Grande Anse River (GRA01), Grande Anse River (GRA02), Jumping Brook (JB01), Little Southwest Brook (NAR02), MacIntosh Brook (GRA03), McGregor Brook (NAR01), Neil Brook (NB01), Still Brook (SB01), South Aspy River (SAR01), and Warren's Brook (WB01). See Appendix Table A4 for percentage of grassland for each stream.

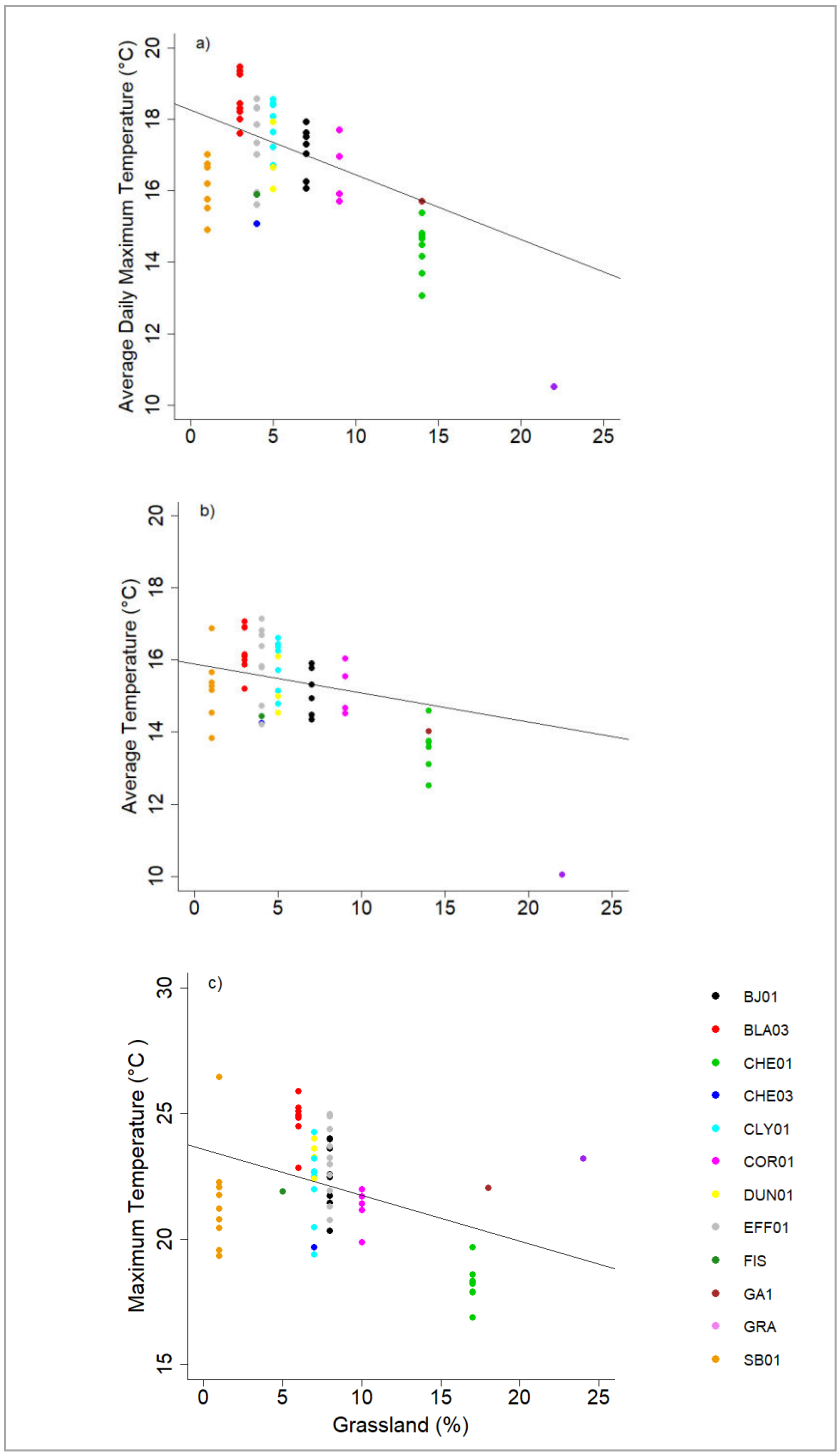

Figure 2.3: Relationships between a) average maximum daily stream temperature, b) average stream temperature, and c) maximum stream temperature to percentage of moose-mediated grassland in 12 streams monitored during summer 2006-2016.

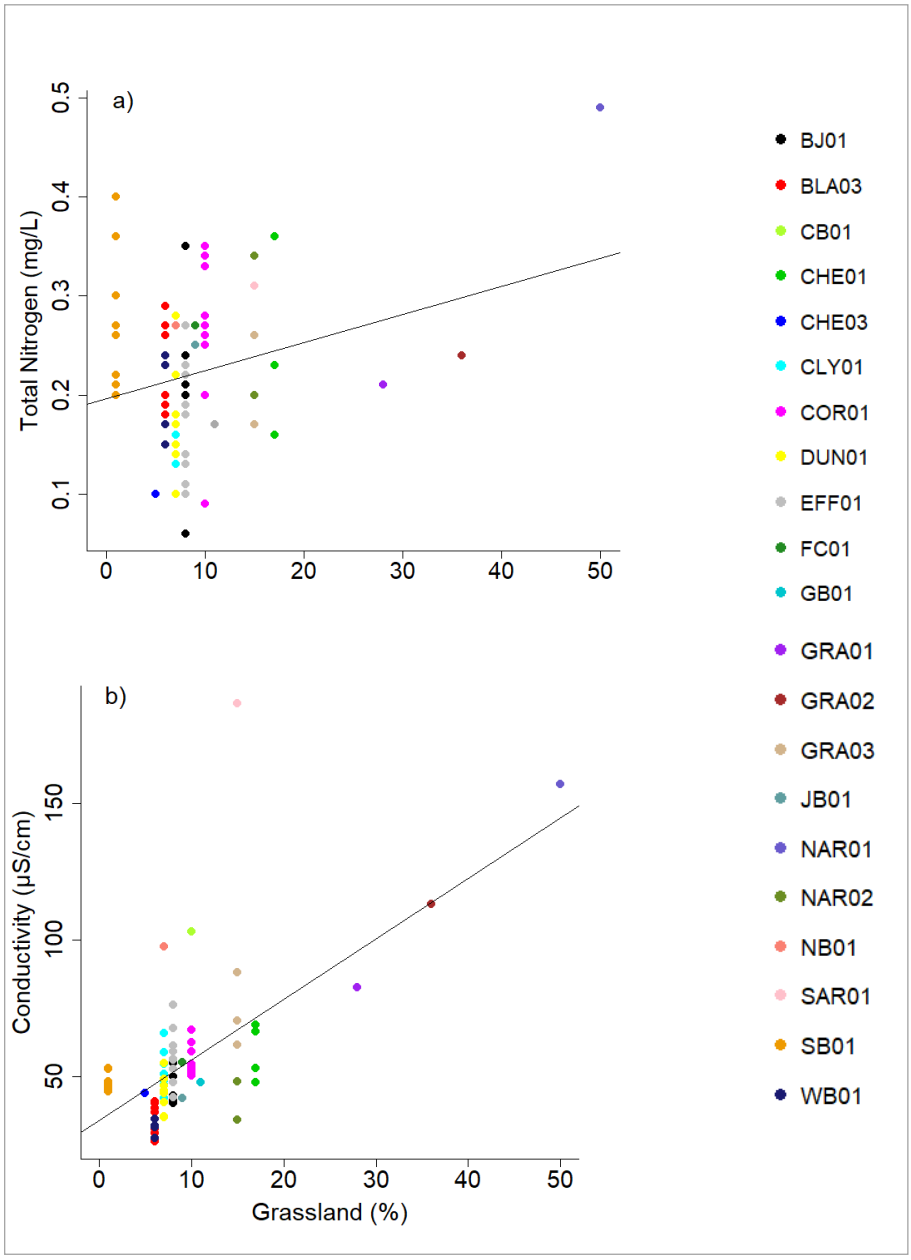

Figure 2.4: Relationships between a) total nitrogen and b) electrical conductivity to percentage of moose-mediated grassland in 21 streams monitored during fall 2005-2014. The results are robust to removal of sites: GRA01, GRA02, and NAR01.

Table 2.1: AIC model selection for effects of grassland on average daily maximum stream temperature, average stream temperature, and maximum stream temperature with environmental variables for 12 streams monitored during summer 2006-2016. Only models with $\Delta AIC_C < 8$ are shown; null models included.

Response	Model description	k	LL	AIC_C	ΔAIC_C	ω AIC_C	R^2
ADM Stream Temperature (˚C)	Grassland + Year + Order + ADM Air Temperature	16	-94.53	232.39	0.00	0.37	0.57
	Grassland + Year + Order + Slope + ADM Air Temperature	17	-92.90	232.81	0.42	0.30	0.59
	Grassland + Year + ADM Air Temperature	14	-98.92	234.23	1.84	0.15	0.50
	Grassland	3	-114.05	234.47	2.08	0.13	0.34
	Grassland + Year + ADM Air Temperature + Slope	15	-98.68	237.16	4.77	0.03	0.51
	Grassland + Year + Order	15	-99.97	239.17	6.78	0.01	0.56
	Intercept	2	-128.39	260.97	28.58	0.00	-
Average Stream Temperature (˚C)	Grassland + Slope	4	-104.94	218.52	0.00	0.49	0.17
	Grassland	3	-106.52	219.41	0.89	0.31	0.13
	Grassland + Slope + Order	6	-104.01	221.39	2.87	0.12	0.19
	Grassland + Order	5	-105.76	222.48	3.96	0.07	0.15
	Intercept	2	-111.12	226.42	7.90	0.01	-
Maximum Stream Temperature (˚C)	Grassland + Maximum Air Temperature	4	-135.40	279.47	0.00	0.87	0.18
	Grassland + Maximum Air Temperature + Order	6	-134.95	293.35	3.88	0.13	0.20
	Intercept	2	-137.57	314.36	34.89	0.00	-

k is number of parameters; LLis log-likelihood; AICc is Akaike information criterion, ΔAICc is difference in AIC between most parsimonious model and subsequent models; ωAICc is Weight of model.

Table 2.2: AIC model selection for grassland effects on total nitrogen and electrical conductivity with environmental variables for 21 streams monitored during summer 2005- 2014 (watershed area was dropped due to VIF>3). Only models with $\Delta AIC_C < 8$ are shown; null models included.

Response	Model description	k	LL	AIC_C	ΔAIC_C	ωAIC_C	R2
Total Nitrogen (mg/L)	Grassland + Year + Order	15	112.99	-188.82	0.00	0.40	0.39
	Grassland + Year	12	108.01	-187.56	1.26	0.21	0.31
	Grassland + Year + Slope	13	109.30	-187.31	1.51	0.19	0.33
	Grassland + Year + Slope + Order	16	113.51	-186.78	2.04	0.14	0.40
	Grassland	3	95.43	-184.56	4.26	0.05	0.10
	Intercept	2	92.76	-181.36	7.46	0.01	-
Conductivity	Grassland + Elevation + Order	7	-347.70	710.89	0.00	0.99	0.57
	Grassland	3	-361.69	729.68	18.79	0.00	0.40
	Intercept	2	-383.01	770.18	59.28	0.00	-

k is number of parameters; LLis log-likelihood; AICc is Akaike information criterion, ΔAICc is difference in AIC between most parsimonious model and subsequent models; ωAICc is Weight of model.

Table 2.3: AIC model selection for total macroinvertebrate abundance and functional feeding groups with environmental variables for 21 watersheds monitored during fall 2005- 2014. Only models with $\Delta AIC_C < 8$ are shown; null models included.

Response	Model description	k	LL	AICc	ΔAIC_C	D^2
Total Abundance (# of individuals)	Grassland + Year + Order + Substrate	18	-1362.37	1400.4	0.00	0.42
	Grassland+ Year + Substrate	15	-1369.76	1401.8	1.40	0.36
	Grassland + Year + Order	14	-1378.29	1408.3	7.90	0.30
	Intercept	2	-1410.71	1414.70	14.30	-
EPT Abundance (# of EPT individuals)	Grassland + Year + Order + Substrate	18	1270.66	1308.7	0.00	0.42
	Grassland + Year + Substrate	15	-1277.65	1309.7	1.00	0.37
	Intercept	2	-1319.52	1323.50	14.80	-
Shredders (%)	Grassland + Year + Order	14	-289.42	608.84	0.00	0.28
	Grassland+ Year + Order + Substrate	18	-289.42	610.10	1.26	0.33
	Intercept	2	-606.63	610.64	1.80	-
Grazers (%)	Grassland + Year + Order + Substrate	16	-334.28	706.56	3.11	0.44
	Grassland + Year + Order	14	-339.64	709.29	5.84	0.36
	Intercept	2	-717.18	721.19	17.74	-
Predators (%)	Grassland + Year + Order + Elevation	15	-321.17	674.35	0.00	0.37
	Grassland + Year + Order	14	-323.04	676.08	1.73	0.34
	Grassland + Year + Elevation	12	-325.21	676.42	2.07	0.31
	Grassland + Year + Substrate + Elevation	16	-321.92	677.85	3.50	0.35
	Grassland + Year + Substrate + Order + Elevation	19	-319.51	679.03	4.86	0.39
	Grassland + Year + Substrate	15	-324.18	680.37	6.02	0.32
	Grassland + Year + Substrate + Order	18	-322.17	682.33	7.98	0.35
	Intercept	2	-680.86	684.86	10.51	-
Filterers	Grassland + Order + Substrate + Elevation	10	-189.24	400.48	0.00	0.27

(%)	Grassland + Order + Substrate	9	-190.64	401.28	0.80	0.25
	Grassland + Substrate + Elevation	7	-193.54	403.08	2.60	0.19
	Grassland + Order + Elevation	6	-194.66	403.32	2.84	0.17
	Grassland + Order	5	-196.30	404.61	4.13	0.14
	Grassland	2	-201.29	405.59	5.11	0.003
	Grassland + Elevation	3	-190.19	406.39	5.91	0.07
	Grass + Substrate	6	-196.29	406.59	6.11	0.14
	Intercept	2	-405.00	409.01	8.53	-
Gatherers (%)	Grassland + Year + Substrate + Order + Elevation	19	-328.99	698	0.00	0.51
	Grassland + Year + Substrate + Elevation	16	-333.04	700.09	2.09	0.46
	Grassland + Year + Order + Elevation	15	-352.23	704.46	6.46	0.42
	Grassland + Year + Order	14	-337.30	704.6	6.60	0.40
	Grassland + Year + Order + Substrate	18	-333.68	705.36	7.36	0.45
	Intercept	2	-717.69	721.69	23.69	-

k is number of parameters; LLis log-likelihood; AICc is Akaike information criterion, ΔAICc is difference in AIC between most parsimonious model and subsequent models; ωAICc is Weight of model

CHAPTER 3: Local-scale effects of hyperabundant moose on headwater stream ecosystems

3.1 Introduction

Trophic interactions between top predators, ungulates, and plant species can have cascading impacts on terrestrial and aquatic ecosystem structure and dynamics (Estes et al. 2011; Ripple and Beschta 2012; Ford and Goheen 2015; Ripple et al. 2016). For instance, when gray wolves (*Canis lupus*) increased in Isle Royale National Park, USA, moose abundance decreased and balsam fir (*Abies balsamea*) growth increased due to decreased browsing pressure of moose (*Alces alces*) (Vucetich and Peterson 2014). Many of these trophic interactions can have impacts that cross local ecosystem boundaries (Estes et al. 2011; Leroux and Loreau 2012). For example, in Yellowstone National Park, USA, loss of riparian vegetation by over-abundant ungulate browsing caused river channel widening and erosion (Beschta and Ripple 2006). Many ungulate species play important roles in connecting terrestrial and aquatic ecosystems via their foraging behaviour (Moss 2015, Bakker et al. 2016). While many studies have investigated the effects of hyperabundant ungulates on the structure and functioning of forest ecosystems with (Kielland and Bryant 1998, Pastor et al. 1993, Pastor et al. 1998, Persson et al. 2005) and without major predators (McLaren et al. 2009, Smith 2007, DeJager et al. 2017, Ellis and Leroux 2017), few studies have investigated impacts of hyperabundant ungulates on aquatic ecosystems (Bakker et al. 2016, but see Beschta and Ripple 2006, Bump et al. 2009, 2017).

To predict the effects of large terrestrial ungulates on stream ecosystems, I determine potential impacts on aquatic ecosystems from research investigating the

impacts of other tree removal processes such as commercial forest harvesting. For instance, high levels of moose browsing creates more open areas by reducing the height of saplings thereby slowing forest regeneration leading to more spruce-moose savannah (Thompson et al. 1992, Pastor et al. 1993, Smith et al. 2010). The removal of the forest canopy has been shown to increase stream temperature by increasing solar radiation inputs (Johnson and Jones, 2000, Gomi et al. 2006, Pollock et al. 2009). Increases in stream temperature in turn leads to increased primary productivity in streams (Kiffney et al. 2003, Wilkerson et al. 2010). For example, Wilkerson et al. (2010) found increased chlorophyll *a* and ash-free dry mass (AFDM) of periphytic algae after forest harvesting, even with 10-m forest buffers around streams. While incident solar radiation is considered the main contributor to periphyton growth, nutrients can also influence stream periphyton (Hillebrande et al. 2002) and large terrestrial ungulates have the potential to influence watershed nutrient flows as well.

Nutrient dynamics in stream ecosystems, such as total nitrogen, are dependent on the surrounding forest landscape (Gundersen et al. 2010). Watersheds with less tree cover may have less rainfall interception by forest canopy resulting in more overland flow and transport of dissolved nutrients (Keenan and van Dijk 2010). The removal of the forest canopy not only influences nutrients, but also dissolved solids entering the stream. For example, in Richardson and Beraud's (2014) global synthesis of forestry impacts on streams found higher levels of total nitrogen and electrical conductivity in streams where the riparian buffers around streams were removed during commercial forest harvesting. In some instances, the removal of riparian vegetation causes increases in nitrogen-fixing

plant species, such as red alder (*Alnus rubra*), thereby increasing nitrogen in streams (Wipfli and Musslewhite 2004).

The loss of riparian vegetation not only alters light fluxes and nutrient dynamics, but the biotic structure of macroinvertebrate assemblages. Many studies examining effects of forest harvesting disturbance found increased abundance and altered macroinvertebrate community structure. Stone and Wallace (1998) found macroinvertebrate total abundance increased even many years after the disturbance likely due to increased nutrient availability supporting higher periphyton biomass. Also, increases in primary productivity have been shown to increase EPT (Ephemeroptera, Plecoptera, and Trichoptera) invertebrate abundance after forest harvesting (Jackson et al. 2007). Additionally, increased periphyton growth after removal of riparian trees can increase abundances of grazing, collector-gatherers, and predator invertebrates (Newbold et al. 1980, Hawkins et al. 1982, Bilby and Bisson 1992, Sweeney 1993, Stone and Wallace 1998). Similarly, the removal or reduction in riparian vegetation among streams decreases litter inputs, specifically altering the quality of organic matter and suspended particulate material, thereby impacting macroinvertebrates such as shredders and filter-feeders (Haefner and Wallace 1981, Sweeney 1993, Stone and Wallace 1998).

The major impacts of forest removal on stream temperature, water chemistry, and stream biota show the importance of riparian and upland vegetation to stream ecosystem functioning. I hypothesize that heavy moose browsing near small streams is modifying the abiotic (stream temperature, nutrients) and biotic (periphyton, macroinvertebrates) functioning in these streams. Given this is the first empirical study of moose impacts on

stream functioning, I use knowledge of forestry impacts on streams to formulate specific predictions about moose impacts on streams. I used percentage of deteriorated boreal forest (hereafter referred to as grasslands) found in the sub-basin in my analysis (see details in methods) to quantify moose impacts on stream ecosystems. I predict that streams with higher levels of moose impacted landscapes will have:

a) higher average daily maximum (ADM), average, maximum, and minimum stream temperatures, as well as higher average daily temperature ranges;
b) higher total nitrogen and electrical conductivity levels;
c) higher periphyton algae biomass measured as chlorophyll *a* and ash-free dry mass (AFDM);
d) higher total and EPT macroinvertebrate abundance, as well as altered macroinvertebrate community structure with more grazers, collector-gatherers, and predatory invertebrates present. Shredding and filter-feeding invertebrates will be lower in grassland streams than forested streams.

In addition, I explore changes in macroinvertebrate taxonomic composition to best describe the communities in the sampled headwater streams.

3.2 Methods

Study Area

The study was conducted in the Cape Breton Highlands, located at the northern part of Cape Breton Island, Nova Scotia which borders both the Gulf of St. Lawrence and Atlantic Ocean (Figure 3.1). I focused on small headwater streams, half of which have relatively high percentage of grasslands (*i.e*. high moose impact) in the surrounding

watershed and the other half are primarily surrounded by intact boreal forest with low moose impact. The tributaries in the moose-mediated grassland habitat originate on the plateau of North Mountain, flowing into either the Grand Anse (GRA04, GRA05), North Aspy (NAR04, NAR05, NAR06), or Red Rivers (RR01, RR02) (Figure 3.2). The forested tributaries, Benjie's Lake Brook (BJ02) and Phillips Cove Brook (PC01), originate on the plateau of the Mackenzie Mountain while the tributaries of Fishing Cove River (FC02, FC03, FC04) originate on the plateau of French Mountain (Figure 3.3). The (Northeast) Margaree River tributaries (MAR01, MAR02) originate on the highland plateau located in the Margaree River Provincial Wilderness Area outside the southern boundary of Cape Breton Highlands National Park (Figure 3.3).

Weather on the Cape Breton Highlands plateau is notably different than lower-lying regions, with rapid changes in temperature and precipitation. The plateau is approximately 400 m above sea level, making for abundant snowfall that stays late into the season (Neily et al. 2003). Elevation ranges for North Mountain, Mackenzie Mountain, French Mountain, and Margaree River plateau are approximately 400-480 m. The geology of the plateau is largely metamorphic and igneous bedrock from the Late Precambiran to Middle Palezoic period, covered by a thin, discontinuous veneer of till and residuum (Baechler and Boehner 2014).

The highlands are part of the Acadian Forest Ecozone, but also contain vast expanses of coniferous forests with mixed and deciduous forest. The plateau of the boreal forest region is characterized by balsam fir, as well as black spruce (*Picea mariana*), white spruce (*Picea glauca*) and white birch (*Betula papyrifera*) (Parks Canada 2009).

The Taiga forest region is likewise located on top of the plateau and is characterized by barren landscape with stunted softwoods and boggy wetlands. Black spruce, balsam fir, and eastern larch (*Larix laricina*) dominate the region with sphagnum moss in open bogs and reindeer lichens making up the drier barren landscape (Parks Canada 2009).

Site Selection

Because I am interested in the effects of moose on stream function, I selected sites with similar biophysical characteristics, except moose impact in their watersheds. Specifically, sites were chosen based on similar size (0.17-0.8 km^2), slope (0.03-0.2), elevation (225-420 m), and substrate size (cobbles vs. bedrock), as well as location (see Appendix B, Table B1). The sites are all located on the plateau of the highland region in the boreal forest, with various amounts of wetlands in the headwater region (see Appendix Table B1). I also chose sites that were accessible in this rugged terrain (< 1 km away from road) and which had minimal human disturbance (*i.e.* sites upstream from road crossings and minimal human footprint). The length of the study reach was standardized at 50 m to adequately sample the aquatic habitat and streamside vegetation of each site.

Headwater streams were first identified using recent landcover data on top of a watercourse dataset in ArcGIS. I then selected 12 potential moose impacted (*i.e.* high percentage of grassland) and 12 forested sites to be verified with field assessments for the above criteria. Many candidate streams were considered unsuitable; therefore, two streams were selected south of CBHNP in the Margaree River Wilderness Area. In the end, I retained 7 streams with sizeable amount of moose-mediated grassland in their

watersheds and 7 streams with little to no moose-mediated grasslands in their watersheds for this study (see Appendix Figure B5 for examples).

Grassland as a Proxy for Moose Effects

In the highlands of Cape Breton, spruce budworm outbreaks during the 1970s and 80s killed up to 90% of the balsam fir forest (Ostaff and MacLean 1989). The regenerating forest consisting of white birch and balsam fir provided an abundant food source for moose, which combined with low levels of predation and disease, allowed moose populations to reach hyperabundance. The combined impacts of high moose densities and intensive spruce budworm outbreaks have altered normal forest succession, converting vast areas of boreal forest into grasslands (Smith et al. 2010). These types of 'moose meadows' or 'spruce-moose savannah' have been observed in other jurisdictions with hyperabundant moose populations such as Newfoundland, Canada (McLaren et al. 2009) and Isle Royale, USA (Pastor et al. 1993).

I obtained current boreal forest land cover data for Cape Breton Highlands from Nova Scotia Department of Natural Resources (NSDNR 2016). The land cover classification conducted by NSDNR was interpreted from aerial photographs and satellite imagery (NSDNR 2016). The area of deteriorated boreal forest termed 'moose meadows' by NSDNR was used as the proxy for moose effects in this study. I used percentage of grassland (*i.e.* moose meadow) in the sub-basin as a proxy for moose effects. To determine percentage of grassland at each stream, I applied sub-basin delineation techniques using 2016 land cover shapefiles digital elevation model (DEM) data, watercourse data (obtained from Parks Canada), and site locations.

Sub-basin delineation is similar to watershed delineation methods used in Chapter 2, employing specific hydrological modelling tools in ArcGIS Desktop 10.2.2 with a few additional steps. First, I delineated all the major watersheds pertaining to this study (Benjie's Lake Brook, Philips Cove Brook, Margaree River, Grande Anse River, North Aspy River, and Red River) using the fill, flow direction, and flow accumulation tools outlined in Chapter 1. After the above watersheds were delineated for all monitoring sites and transformed into polygons, I created a raster map of each watershed using the raster calculator derived from the flow accumulation map including only cells that exceed flow accumulation ≥ 1000 cells, ensuring that small headwater streams would be selected (Mackenzie 2016). Then, the streamlink tool was used on the stream raster map producing a map with unique ID numbers for each stream segment or link (Mackenzie 2016). Lastly, I used the watershed tool inputting flow direction and the streamlink map as pour point targets to delineate sub-basins within the watershed.

After the sub-basins were created for each site, I constructed polygons for each sub-basin and extracted the sub-basin of interest (my study sites). I then digitized shapefiles for each sub-basin for my study, tracing over the polygon and creating a perpendicular line at the downstream boundary of the study site. This was done because most of the study reaches were located upstream from the confluence and not at the confluence where the sub-basin polygons originate. Finally, I intersected each sub-basin polygon with the 2016 land cover data to calculate the percentage of grassland per sub-basin. Additional land cover variables, such as percentage of upland alders and wetlands were also calculated from the GIS data.

Stream Temperature Data Collection

Continuous temperature was monitored hourly for the chosen sites using Hobo™ water temperature pro V2 data loggers. These loggers, protected with white PVC constructed pipe housing as to limit direct solar radiation, were installed in streams and anchored in place with rebar. The loggers were placed in a well-mixed pool at the downstream boundary of the study reach ensuring the logger was not directly flush with the streambed. The loggers were installed in all 14 streams beginning July 4, 2016 and ending October 3, 2016. Hobo logger malfunctioning occurred at four sites, however, three of these sites had Diver loggers in place reading both temperature and conductivity. Therefore, I used the temperature data from the Diver loggers for three sites after determining only minor variability existed between the two types of loggers (see Appendix Figures B1, B2).

I calculated summary statistics for stream temperature at 13 sites monitored for 82 days from July 4-September 22, 2016 (Appendix Table B3). I calculated average daily maximum temperature (ADMT), average stream temperature, and average daily temperature range, the difference between the maximum and minimum daily temperature. Maximum and minimum stream temperatures were also extracted from the dataset for analysis.

Total Nitrogen and Conductivity Data Collection

Water samples for total nitrogen were collected every month for each site (except for Philip's Cove in September), adhering to Canadian Aquatic Biomonitoring Network

(CABIN) protocols for wadable streams (Environment Canada 2012). Approximately 125ml of stream water was taken at the downstream boundary of the study reach for total nitrogen analysis. The water samples were kept in a cooler and analyzed by the Environmental Services Laboratory for the Nova Scotia Health Authority in Halifax, Nova Scotia. Electrical conductivity (measured as specific conductance at 25°C) was analyzed in the field using a Myron Ultrameter Model 6P. The site Philip's Cove Brook (PC01) was not sampled during September due to site access issues. In addition to directly monitoring conductivity, I installed six CTD-Diver Loggers that measure temperature and conductivity hourly. They were installed in three forested streams (PC01, MAR01, FC04) and three grassland streams (NAR05, GRA05, RR01). The average and maximum conductivity values were calculated for these sites, however, due to lack of model convergence they were removed as an additional measure of conductivity.

During data collection, road construction for the Cabot Trail Rehabilitation project began on Mackenzie Mountain. Therefore, the data pertaining to the sites found on Mackenzie Mountain, Benjie's Lake Brook (BJ02) and Phillip's Cove Brook (PC01), had to be removed from conductivity analysis due to contamination. For instance, the conductivity values far exceeded levels detected in Benjie's Lake Brook years prior (see Appendix Figure B3 for details). Despite elevated electrical conductivity due to road construction, BJ02 AND PC01 sites did not exceed 500 µS/cm as suggested as the upper limit for inland freshwater systems (EPA 2012). Thus, I retained these sites for all other analyses (i.e. stream temperature, total nitrogen, periphyton biomass, and macroinvertebrate).

Periphyton Biomass Data Collection

A five-week colonization study was conducted on periphyton biomass in the 14 study streams beginning on July 4 and ending August 9, 2016. Periphyton were assessed using artificial substrates, which were 10.8 x 10.8 cm (116.64 cm^2) unglazed ceramic tiles (2) fixed to a standard sized brick. There were five bricks per 50 m study reach for a total of 10 tiles per site. The 50 m study reach was divided into five, 10 m intervals with one brick installed in roughly the middle of each interval. The brick was placed in a pool with good flow to ensure it would be submerged throughout the colonization period.

At the end of the colonization period, each brick was pulled from the stream and all macroinvertebrates were removed. The tiles were then scraped using a sterilized razor blade, as well as scrubbed vigorously with a hard-bristled brush to removal all periphyton before they were rinsed with distilled water into a small basin. A ~500 ml slurry was created for all scraped tiles in each study stream and filtered through pre-combusted, pre-weighed 47mm glass fibre filters (GF/F 1.2 µm) using a hand-held vacuum pump. The filters were placed in pre-labelled aluminium foil and put into an ice cooler from which they were later transferred into a -20˚C freezer. For each site, half of the filters were analyzed for chlorophyll *a* and half for ash-free dry mass (AFDM). I followed Hauer and Lamberti's (2011) methods for chlorophyll *a* and AFDM analysis.

Macroinvertebrate Data Collection

Macroinvertebrate sampling was conducted between October 3 and 13, 2016 complying with CABIN protocols for wadable streams (Environment Canada 2012). I first evaluated

various aspects of the study reach, such as % canopy coverage, dominant streamside vegetation, and aquatic habitat types. I then took my water samples and measured basic water quality parameters. Next, I conducted the macroinvertebrate sampling by travelling in a zigzag pattern upstream, dragging the collection net and kicking the substrate for a period of three min (Environment Canada 2012). To account for the entire study reach, I kick-netted the substrate for one min, three times in randomly chosen intervals of the 50 m study reach. After kick-netting, I sorted the sample by rinsing and discarding any large debris with a sieve over a basin. I transferred the sample into jars labelled with the date and site. The sample was first preserved using buffered 10% Formalin, then rinsed and transferred into 90% Ethanol within 48-hr period. After the invertebrates were collected, I conducted in stream channel measurements such as depth, bankfull width, wetted width, and velocity. Stream velocity was conducted using the velocity head rod method as outlined in the CABIN field manual (Environment Canada 2012). These channel measurements, as well as reach characteristics were also recorded early on during initial stream surveys. After the channel measurements were made, I conducted the 100-pebble count where 100 rocks are randomly selected in the erosional zone (Environment Canada 2012). This was done in the same zigzag pattern as the macroinvertebrate collection and the intermediate axis of the substrate was measured.

After the invertebrate sample was transferred to ethanol and sorted further in the laboratory to ensure adequate removal of all debris, they were sent to the BioTech Taxonomy Laboratory in Smithtown, New Brunswick for identification at the family level. Macroinvertebrate raw data were entered into the online CABIN database. I used

the database to determine metric data pertaining to total abundance, EPT abundance, and functional feeding groups. There was unseasonably heavy rainfall during macroinvertebrate collection in the Fishing Cove River streams (FC02, FC03, FC04) and Margaree River streams (MAR01, MAR02). Consequently, I did not include these sites in the analysis of moose effects on macroinvertebrate community structure (see Appendix Table B9 for data on flooded forested sites).

Moose Browse Surveys

As an additional measure of moose effects in the sub-basin, I conducted four, 50m long transect moose browse surveys perpendicular to my study streams in conjunction with the invertebrate collection in October 2016. I randomly chose four intervals in the 50m study reach and ensured two transects per side of the stream. Moose browse was measured using the browse severity classification table in Smith et al. (2010), which outlines criteria used when deciding browse levels. The dead classes used were lightly browse (1), moderately browsed (2), severely browse (3), and dead (4) and height was recorded.

Data Analysis

I used general linear models with percentage of grassland as the fixed effect to test my predictions about moose impacts on stream temperature and periphyton biomass. For total nitrogen and conductivity, I used a mixed model with both fixed (*e.g.* percentage of grassland) and random (*e.g.* site) effects. I included site as a random factor in these models as the data had a nested structure with multiple samples per site. The invertebrate

data were over-dispersed, therefore, I used a generalized linear model with a negative binomial distribution and a log-link for all invertebrate models.

First, I measured the variance inflation factor (VIF) to test for multicollinear covariates (*i.e.* VIF > 3) from each model set. I then used Akaike Information Criterion corrected for small sample size (AIC_C) to determine the weight of evidence in support of an effect of moose (*i.e.* percent grassland) on stream temperature, total nitrogen, conductivity, periphyton biomass, and macroinvertebrate taxa/metrics (total abundance and functional feeding groups). I also present R^2 or deviance explained (D^2; for macroinvertebrate data) as an additional measure of model fit (Guisan and Zimmermann 2000). Models with pretending variables (sensu Anderson 2008) or uninformative parameters (sensu Arnold 2010) were removed from each model set.

Temperature Models: During the analysis, I initially included percentage of wetland and stream discharge in the models. However, they were both found to be pretending variables (*sensu* Anderson 2008) and removed from all models. I tested relationships between grassland with the following response variables; ADM stream temperature, average stream temperature, maximum stream temperature, minimum stream temperature, and average daily temperature range.

Total Nitrogen and Conductivity Models: To account for natural variability, stream discharge and percentage of upland alders in the sub-basin were included as covariates in total nitrogen and conductivity analysis. I found stream discharge to be a pretending variable, thus it was removed from all analyses. I tested relationships between fixed

effects (grassland and alder percentage), as well as random effects (site) with total nitrogen and conductivity.

Chlorophyll a and Ash-free dry Mass Periphyton Models: To account for natural variability in chlorophyll *a* and periphyton ash-free dry mass (AFDM), I included the covariates stream discharge and substrate size. I tested relationships between grassland, stream discharge, and substrate size with chlorophyll *a* and AFDM.

Macroinvertebrate Models: The natural variability of streams was accounted for by including dominant streamside tree species, substrate size, and average stream discharge as covariates in the models. Average stream discharge was calculated based on velocity x width x depth measurements taken during the initial and final stream surveys under normal flow conditions. I tested relationships between grassland, dominant tree species, stream discharge, and substrate size with family level taxa, abundance metrics, and functional feeding groups.

3.3 Results

Moose Impacted Landscape Assessment

I found a gradient of moose-mediated grassland located at the North Mountain sites, ranging from 28% for Red River stream (RR01) to 69% for North Aspy River stream (NAR05) (Appendix Table B1). While I found very low levels in the forested sites, with only Fishing Cove River stream (FC03) having 4% grassland while the other sites had no levels of grass detected (Appendix Table B1). In accordance with these results, I found

the average number of trees browsed adjacent to North Mountain streams was 238 (± 96 SD), while just 70 (± 50 SD) for forested streams (see Appendix Table B2).

Stream Temperature

Over the course of the study period (July 4 – September 22), I found no evidence to suggest that stream temperatures are warmer at grassland sites than at forested sites (Table 3.1; *i.e.* model with grassland ranks below the intercept-only model). I found similar results for all stream temperature parameters with average daily maximum, average, maximum, and minimum temperatures showing with no relationship to grassland at 13 sites (Table 3.1; note: 1 site dropped because of logger malfunction). The highest average daily maximum and average temperatures were recorded at the grassland site North Aspy River stream (NAR04), while the highest average temperature was recorded at the grassland site North Aspy River stream NAR06. The highest minimum value was recorded at the grassland site Red River stream (RR01). Likewise, the lowest average, maximum, and minimum temperature were all recorded at the forested site Margaree River stream (MAR02).

I did find evidence that grassland streams have higher daily temperature ranges (Figure 3.4). The highest steam temperature range was recorded at the grassland site NAR04 with 4.69 ºC, while the forested site Phillips Cove (PC01) had the lowest temperature range at 1.27 ºC. The top ranked model to explain variation in stream temperature ranges included grassland (Table 3.1; $R^2 = 0.34$).

Total Nitrogen and Conductivity

For the 14 study streams, I found a positive relationship with total nitrogen and grassland (Figure 3.5A). The average total nitrogen value for forested streams was 0.21 mg/L (± 0.09 SD) and for grassland streams it was 0.44 mg/L (± 0.17 SD). The recorded values ranged between 0.1 mg/L for the forested site Margaree River stream (MAR02) and 0.84 mg/L for the grassland site Grande Anse River stream (GRA05). The top model for total nitrogen included percentages of grassland and alders, explaining 67% variation, with some site-level differences (conditional R^2 of top model was 69%) (Table 3.2). My top model shows a positive relationship with both grassland and alders in the sub-basin (Table 3.2).

For conductivity, I also found a positive relationship with grassland for 12 study streams (Figure 3.5B; note: two streams dropped because of disturbance upland). Conductivity was on average higher at moose impacted streams than forested streams, with an average of 78.89 (± 39 SD) and 42 (± 9 SD), respectively. The highest conductivity was recorded at the grassland site North Aspy River stream (NAR04) at 186.36 µS/cm, while the lowest conductivity was recorded at the forested site Fishing Cove River stream (FC03) at 30.46 µS/cm. The top ranked model for conductivity included grassland, explaining 31% of the variance in conductivity. I found substantial site-level differences in conductivity (conditional $R^2 = 0.88$) (Table 3.2).

Periphyton chlorophyll a and AFDM

Counter to my prediction, I found a negative relationship with periphyton chlorophyll *a* and grassland in the 14 headwater streams (Figure 3.6). Chlorophyll *a* was lower for the

seven moose-mediated grassland sites (mean 2.61 (±1.10 SD) µg/cm^2) than the seven forested sites (mean 13.89 (± 11.95 SD) µg/cm^2) (Figure 3.7a). The lowest levels of chlorophyll *a* were found at the grassland site North Aspy River stream (NAR04) at 1 µg/cm^2, while the highest were found at the forested site Fishing Cove River stream (FC03) at 31 µg/cm^2. The top model included grassland only and explained 28% of the variation in chlorophyll *a* (Table 3.3).

Although, there were higher amounts of chlorophyll *a* in forested streams, I found comparable levels of periphyton ash-free dry mass (AFDM) (Table 3.7b, Table 3.3). AFDM was similar for all sites with 0.03 g/m^2 (± 0.01 SD) for the seven grassland sites and 0.04 g/m^2 (± 0.02 SD) for the seven forested sites. The highest level AFDM were found at the forested site Margaree River stream (MAR02) at 0.074 g/m^2, whereas the lowest level was found at the grassland site North Aspy River stream (NAR04) at 0.023 g/m^2.

Macroinvertebrates

Taxonomic composition

The headwater streams sampled had approximately 56 different family level taxa. 35 of these taxa were not included in the analysis as they had less than 10 individuals and greater than seven sites had zero counts. Therefore, 21 family level raw abundance data were analyzed for moose effects. Out of these 21, I found evidence that abundance for only four of these taxa differed between grassland and forested sites. The abundance of Baetidae, Ephemerellidae, Capniidae, and Philopotamidae had a positive relationship with percentage of moose-mediated grassland (Figure 3.8, Table 3.4). The grassland site North

Aspy River stream (NAR06) had the highest number of Baetidae at 81 individuals, while NAR05 had the highest number of Ephemerellidae recorded at 207 individuals. The lowest number of both families was recorded at the forested site Philips Cove Brook (PC01). The highest number of individuals of the stonefly, Capniidae, was found at the grassland site Grand Anse River stream (GRA05), while the forested site Benjie's Lake Brook (BJ02) had only 5 individuals. Finally, the highest number of individuals of the caddisfly, Philopotamidae, were found at the grassland site North Aspy River stream (NAR05), while the lowest was found at the forested site Phillips Cove Brook (PC01). The total abundance of all 21 family level taxa for two forested and seven moose impacted sites can be seen in Appendix Figure B4.

The top ranked models for Baetidae and Philopotamidae included grassland and stream discharge as covariates, explaining 75% and 74% of the deviance, respectively (Table 3.4). The Ephemerellidae and Capniidae top models included only grassland, explaining 36% and 25% deviance, respectively (Table 3.4).

Abundance Metrics

I found no evidence to suggest grassland streams have higher total abundance of macroinvertebrates than forested streams (Figure 3.9). The seven grassland streams (NAR04-06, GRA04-05, RR01-02) had an average number of 1,031 individuals (± 294 SD), while the two forested streams (BJ01, PC01) had a comparable average number of individuals at 928 (± 776 SD). The highest abundance of macroinvertebrates was found at the forested site Benjie's Lake Brook (BJ02) with 1,476 individuals, while the lowest abundance was found at Phillips Cove Brook (PC01) with 379 individuals. The top model

for total abundance included grassland and dominant tree species (D^2= 0.80, ΔAIC = 0.00) (Table 3.4). I removed models with stream discharge and substrate size as covariates from the model set as these covariates were pretending variables (*sensu* Anderson 2008). The total number of individuals increased from grass/fern dominated streams to alder dominated, then decreased in abundance when streamside vegetation dominance went from alder bushes to white birch and balsam fir (Appendix Table B10).

EPT abundance also did not differ significantly between the grassland and forested streams (Figure 3.9), with an average number of 649 individuals (± 183 SD) and 414 individuals (± 310 SD), respectively. The highest number of EPT individuals was found at the grassland site North Aspy River stream (NAR04) with 892, while the forested site Phillips Cove Brook (PC01) had the lowest with only 194 individuals. Similar to total abundance, the top model for EPT abundance included grassland and dominant tree species (D^2= 0.85, ΔAIC = 0.00) (Table 3.4). Again, models with stream discharge and substrate size as covariates were removed from the model sets as these were pretending variables. Likewise, with total abundance, EPT abundance increased in alder dominated streams compared with grass/fern dominated streams, then decreased in abundance when dominated streamside vegetation went from alder bushes to white birch and balsam fir (Appendix Table B10).

Functional Feeding Groups

For many of the sites, collector-gathering invertebrates were the most dominant feeding group, followed by predators and shredding invertebrates (Figure 3.10). The high number of mayflies (Baetidae and Ephemerellidae) and aquatic worms (Lumbriculidae)

contributed to the dominance of the collector-gatherers, while the high number of midges (Chironomidae) both contributed to collector-gatherers and predators. The stoneflies, Leuctridae, Capniidae, and Nemouridae contributed most to the shredders, while the high number of riffle beetles (Elmidae) and net-spinning caddisflies (Hydropsychidae) contributed to grazers and filterers, respectively.

I found little evidence that community structure in grassland streams differed from forested streams. However, there is evidence to suggest that predatory invertebrates may be more abundant at the two forested sites (Figure 3.11). Mean predator abundance was 62 (± 7 SD) for the forested sites and 30 (± 4 SD) for the grassland sites. The highest levels of predators were found at the forested site Benjie's Lake Brook at 66 individuals, while the grassland site Grande Anse River stream (GRA05) only had 22 individuals.

The top ranked model for predatory macroinvertebrates included % grassland and explained 70% of the variation in predatory macroinvertebrates (Table 3.4). I found no evidence for a relationship between other functional feeding groups and % grasslands. However, I found evidence that stream discharge is positively related to shredding and filtering invertebrates, while negatively related to gathering invertebrates (Appendix Table B10). In addition, I found evidence that dominant tree species is related to shredding invertebrates, showing an increase in abundance as dominant streamside vegetation moves from grass/ferns to alder dominated (Appendix Table B10).

3.4 Discussion

My study provides one of the first empirical assessments of the effects of large terrestrial ungulates on headwater stream ecosystem functioning. Similar to evidence from Isle

Royale (McInnes et al. 1992), Scandinavia (Persson et al. 2005) and Newfoundland (Ellis & Leroux 2017), in the Cape Breton Highlands, selective moose browsing has decreased the abundance of balsam fir, white birch, mountain ash, and maples, while increasing the abundance of grasses, ferns, herbs, and shrubs. I show that these moose-mediated changes to boreal forests can cascade to influence stream temperature, total nitrogen, conductivity, and macroinvertebrates in adjacent streams.

I found evidence that moose impacted streams (*i.e.* higher percentage of grassland) have less stable temperature regimes than forested streams (Figure 3.4). The average daily temperature range had greater diel fluctuations for grassland streams than for forested streams, potentially demonstrating that plant species community influences the amount of solar radiation that is reaching streams. Specifically, I observed that forested streams had extensive riparian vegetation with generally high amounts of riparian shade, whereas many grassland streams had lower amounts of riparian vegetation (approximately <10m buffers before reaching into grassland dominated landscape) with variable shade. For instance, forested streams often had mature balsam fir and white birch overhanging streams, while this was less frequent for many grassland streams that had grasses and ferns as dominant streamside vegetation. The diurnal cycle of stream temperature is mainly influenced by direct solar radiation (Herbert et al. 2011), with studies demonstrating solar radiation as the principal cause of elevated stream temperature via forest harvesting (Johnson and Jones 2000, Gomi et al. 2006). Furthermore, it has been shown that tree height influences the amount of shade reaching a

stream with taller vegetation being more effective at moderating stream temperature regimes than shorter vegetation (MacDonald et al. 2003).

In agreement with my prediction on nutrient influences, I found that total nitrogen was higher in grassland streams relative to forested streams (Figure 3.5a, Table 3.2). There maybe several reasons why I observed higher total nitrogen in streams with higher percentages of grassland. First, the nitrogen retention of grass is lower than that of tree species commonly found in the boreal forest (*e.g.* balsam fir, white birch, mountain ash). For instance, Simmons et al. (1992) found that forested riparian buffers had 80% nitrate reduction ability via retention, while Lee et al. (2004) discovered the effectiveness of grassland buffers to be only 61%. Therefore, grassland habitat will have less retention and more surface runoff in the riparian zone, thereby contributing to higher levels of nitrogen. Secondly, plant species composition in the sub-basins may be playing an important role. Alders are nitrogen fixing plant species responsible for increases in nitrate in streams via groundwater (Callahan et al. 2017). Thus, high levels of alders at moose impacted sites further increase nitrogen subsides in these streams and help explain some of the variation in total nitrogen in the study streams (Table 3.2).

Also in line with my predictions on water quality influences, I found that electrical conductivity was higher in grassland streams relative to forested streams (Figure 3.5b, Table 3.2). Loss of forested habitat has long been shown to influence the concentrations of dissolved solids of stream water (Graynoth 1979). For example, Reuss et al. (1997) reported higher levels of electrical conductivity leaching from clear-cut forests several years after forest removal. Therefore, higher conductivity levels in

grassland streams indicate that surface runoff may be more pronounced due to loss of woody vegetation and understory communities, thereby contributing to ion burden in these streams. I did, however, observe high inter-site variability (conditional $R^2 = 0.88$) in the stream conductivity, which suggests that there are likely other site-specific factors (*e.g.* geology, groundwater supply) that may be influencing the concentration of dissolved solids in stream water.

Counter to my prediction on stream biota responses, periphyton chlorophyll *a* was higher in forested streams than in grassland streams (Figure 3.7, Table 3.3). Consequently, I found no evidence for moose impacts on stream periphyton. An alternative explanation for this result is that periphyton are limited by other factors not accounted for in my study such as nutrients, light duration and intensity, temperature fluctuations, discharge, and grazing pressures (Stevenson et al. 1996). While light and nutrients tend to be the main drivers of periphyton growth, grazing invertebrates have a strong effect on the abundance and distribution of periphyton biomass (Taylor et al. 2002). Based on my data, I may speculate about the potential for grazing or reduced grazing to relate to my findings. My results indicate that predatory invertebrates may be higher in forested streams than grassland streams (Figure 3.11, Table 3.4). Predators can exert top-down control in community structure either through direct predation or non-lethal effects through reduced foraging (Schmitz et al. 1997). Predatory invertebrates, such as stonefly nymphs, commonly prey upon grazing invertebrates (Allan and Flecker 1988) and have been shown to exert a stronger influence on prey abundance than vertebrate predators such as brook trout (Wooster 1994). Therefore, higher predators in

forested streams could be reducing grazing ability thereby contributing to decreased grazing pressures and higher periphyton biomass. Consequently, future work should quantify trophic dynamics along with periphyton standing stocks in order to better decipher potential moose impacts on small streams.

The total and EPT macroinvertebrate abundances, as well as most macroinvertebrate functional feeding groups did not differ between grassland and forested streams. Increases in total and EPT abundance were attributed to dominant streamside vegetation, with higher numbers found at streams with tall shrubs, such as speckled alders (*Alnus rugosa*) and lower numbers at white birch and balsam fir dominated streams (Appendix Table B10). Alders are pioneer species that have been shown to increase macroinvertebrate abundance relative to conifer dominated streams in headwater streams in southeastern Alaska (Piccolo and Wipfli 2002).

While total EPT abundance did not differ between study sites, the abundance of several EPT taxa were related to grassland in the sub-basin. The mayflies, Baetidae and Ephemerellidae, were found to be higher in moose impacted streams (*i.e.* grasslands) than forested streams, while the stonefly, Capniidae, and the caddisfly, Philopotamidae, were also found to be higher in grassland streams than forested streams. These families are typically characterized as collector-gatherers and grazers feeding on detritus and algae (Thorp and Covich 2010). The higher levels of grazing taxa could be contributing to the lower levels of periphyton recorded, while increases in the collector-gatherer taxa could be attributed to an increased food supply of fine particulate organic matter (FPOM) in depositional areas (Merritt and Cummings 1996). For instance, Baetidae is associated

with high quality food sources (Thorp and Covich 2010) and maybe influenced by the presence of speckled alders in grassland streams. Although, I did find evidence indicating the above macroinvertebrate taxa and predatory invertebrates differed for grassland streams relative to forested streams, given that I had few data points for forested streams, future work should aim to better characterize the gradient of potential moose impacts on streams. Such work would include more areas of low and high moose impacts, as well as areas with intermediate moose impacts in order to provide a stronger test of moose impacts on macroinvertebrates and other stream properties.

In summary, my study is one of the first investigations of terrestrial ungulate impacts on stream ecosystem structure and functioning. I highlight the importance of riparian and upland vegetation to stream ecosystems by linking current knowledge on forest removal via harvesting to intense herbivory by moose. The degradation of adjacent boreal forest ecosystems can cross ecosystem boundaries influencing stream temperature (Pollock et al. 2009), nutrients, water quality (Richardson and Beraud 2014), and stream biota (Stone and Wallace 1998). My results suggest that the loss of treed stream riparian zones due to moose are decreasing stream temperature stability, as well as increasing total nitrogen and dissolved solids entering the stream. In addition, macroinvertebrate taxa, such as Baetidae, are found in higher abundances conceivably due to the high levels of streamside alder patches on North Mountain sites. These plants benefit grassland stream ecosystems by supplying nutrients to the stream and positively impacting aquatic communities by enriching food sources for macroinvertebrates potentially supporting local fish communities (Piccolo and Wipfli 2002).

Despite lack of boreal forest regeneration due to moose over-browsing the landscape of North Mountain, pioneer species such as alder potentially are mitigating harmful alterations to stream ecosystems. While I have current data on upland alder stands, my knowledge on streamside alder stands is lacking, thus potentially influencing my ability to detect moose impacts on stream ecosystems. It is possible that the prevalence of alders on North Mountain is facilitated by the presence of hyperabundant moose. As noted by Smith (2007), areas severely browsed by moose appear to be in alternate state of succession. The lack of forest regeneration prevents conifers to reach sufficient heights to block out sunlight, making it difficult for shade-intolerant shrubs to be killed. Thus, moose maybe influencing the abundance and distribution of unpalatable pioneer species, such as speckled and green alders. Additionally, ferns and grasses, such as the prevalent *Calamagrostis*, are speculated to maintain abundance even with decreasing moose populations (Smith 2007). Therefore, grasses and alders may be the alternative stable state potentially outcompeting the over-browsed balsam fir and white birch saplings and impacting a myriad of other ecological functions and ecosystems.

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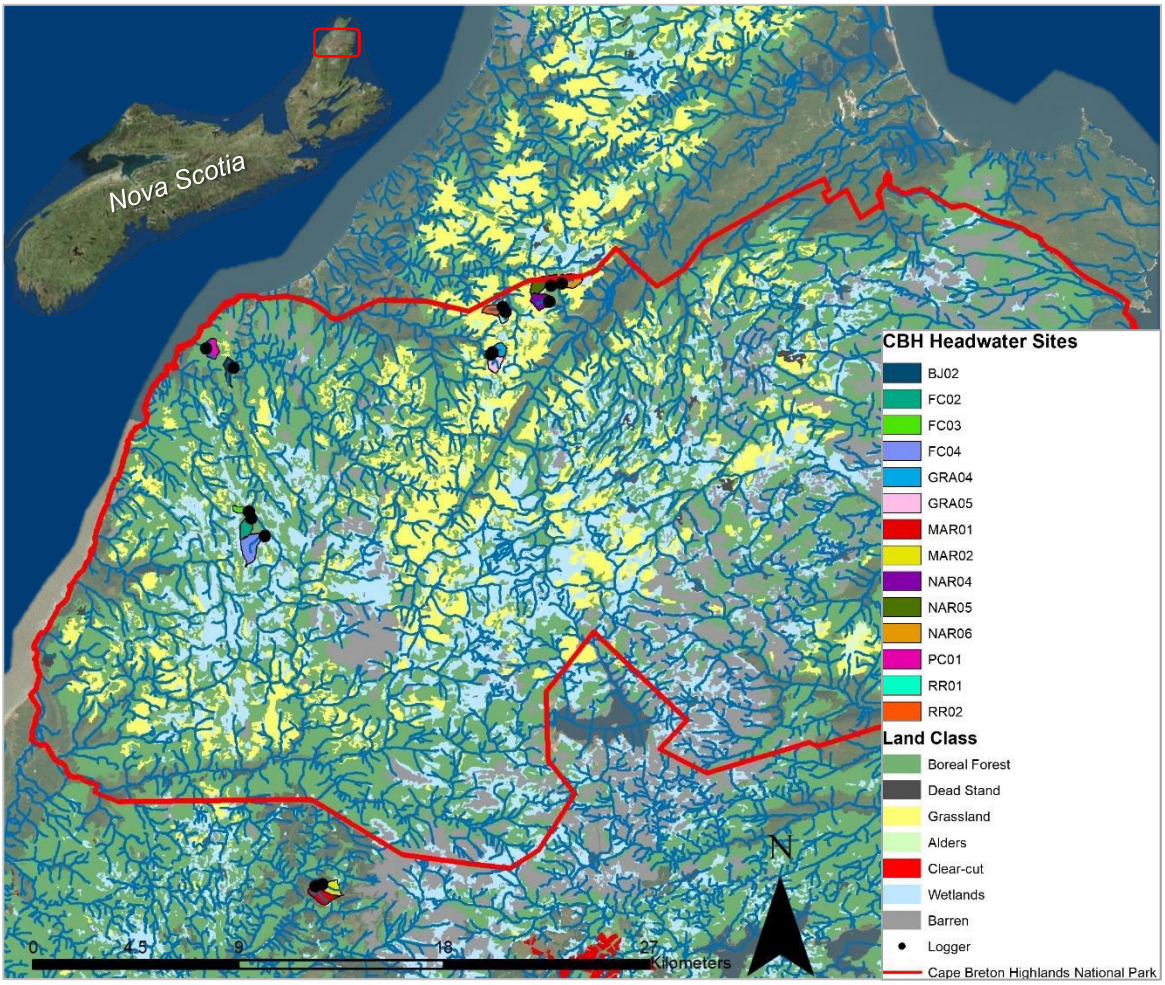

Figure 3.1: Headwater stream sites located in Cape Breton Highlands, Nova Scotia. The grassland streams are Grande Anse River (GRA04, GRA05), North Aspy River (NAR04, NAR05, NAR06), and Red River (RR01, RR02). The forested streams are Benjie's Lake Brook (BJ02), Fishing Cove River (FC02, FC03, FC04), Margaree River (MAR01, MAR02), and Philip's Cove Brook (PC01). Base Map Source: ESRI; Data layer sources: Nova Scotia Department of Natural Resources (NSDNR) 2016 and Parks Canada.

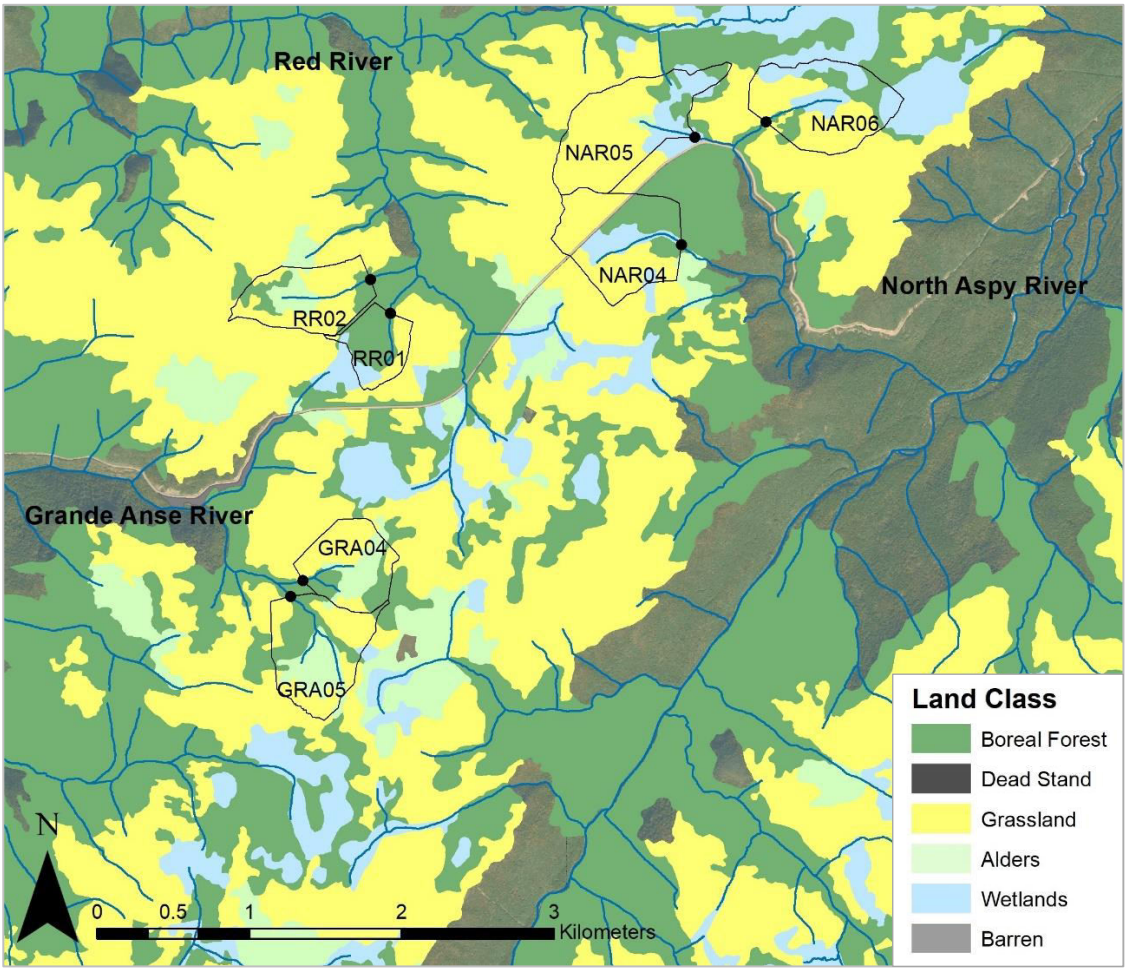

Figure 3.2: The locations of 7 grassland streams on North Mountain, Cape Breton Highlands National Park. The basin names are Grande Anse River (GRA04, GRA05), North Aspy River (NAR04, NAR05, NAR06), and Red River (RR01, RR02). Data layer sources: Nova Scotia Department of Natural Resources (NSDNR) 2016 and Parks Canada.

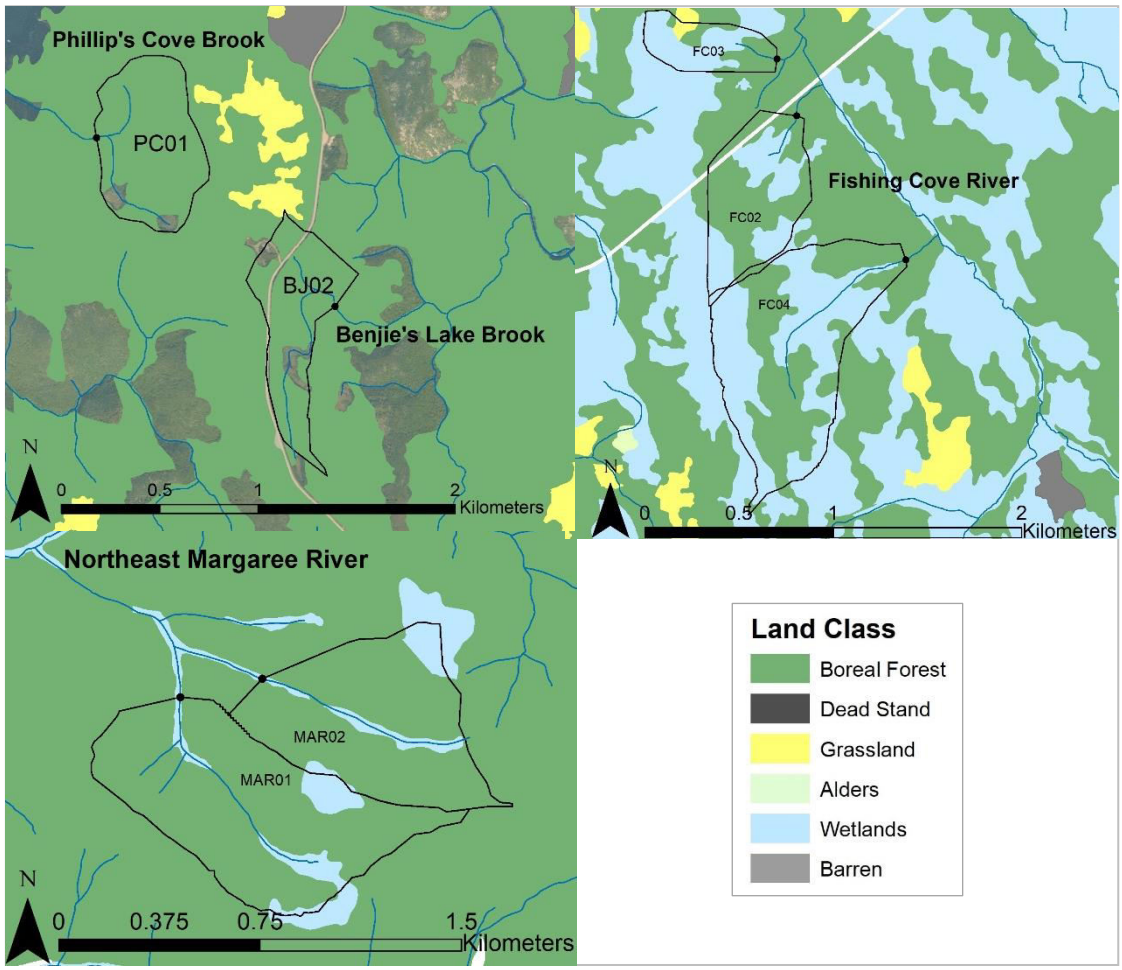

Figure 3.3: The locations of 7 forest streams located in various regions of the boreal forest of Cape Breton Highlands. The basin names are Benjie's Lake Brook (BJ02), Fishing Cove River (FC02, FC03, FC04), Margaree River (MAR01, MAR02), and Philip's Cove Brook (PC01). Data layer sources: Nova Scotia Department of Natural Resources (NSDNR) 2016 and Parks Canada.

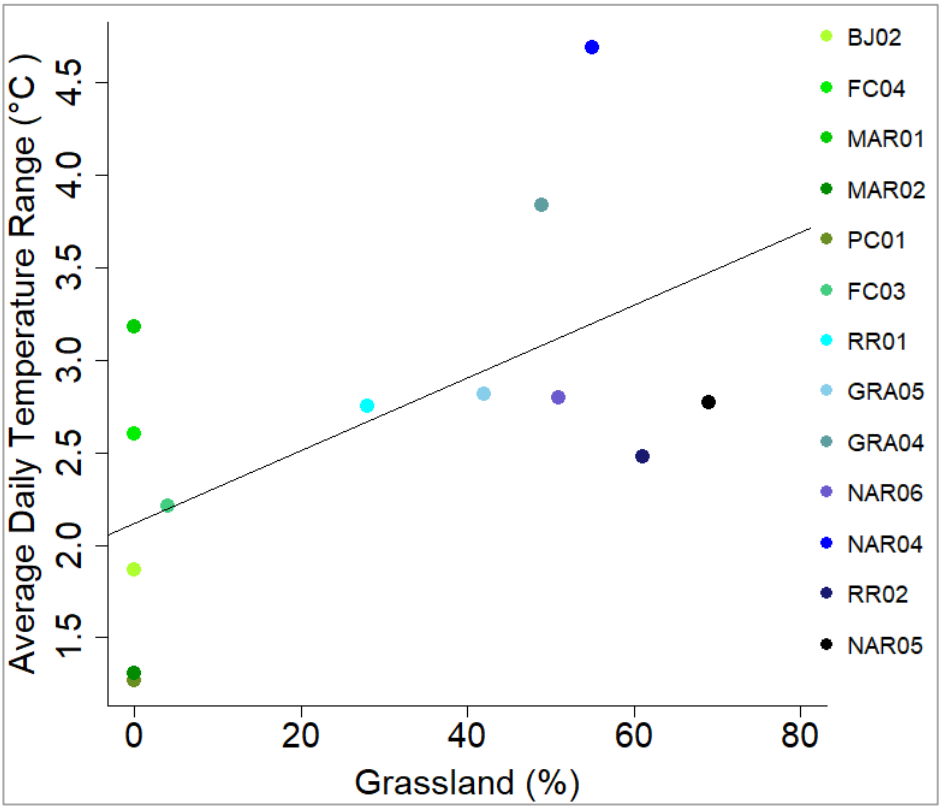

Figure 3.4: Relationship between grassland (%) in the sub-basin and average daily temperature range for 13 headwater streams monitored July-September 2016. **Sites included:** Benjie's Lake Brook (BJ02), Grande Anse River streams (GRA04, GRA05), North Aspy River streams (NAR04, NAR05, NAR06), Margaree River streams (MAR01, MAR02), Philip's Cove Brook (PC01), Red River streams (RR01, RR02), and Fishing Cove River streams (FC03, FC04) *FC02 absent due to logger failure.

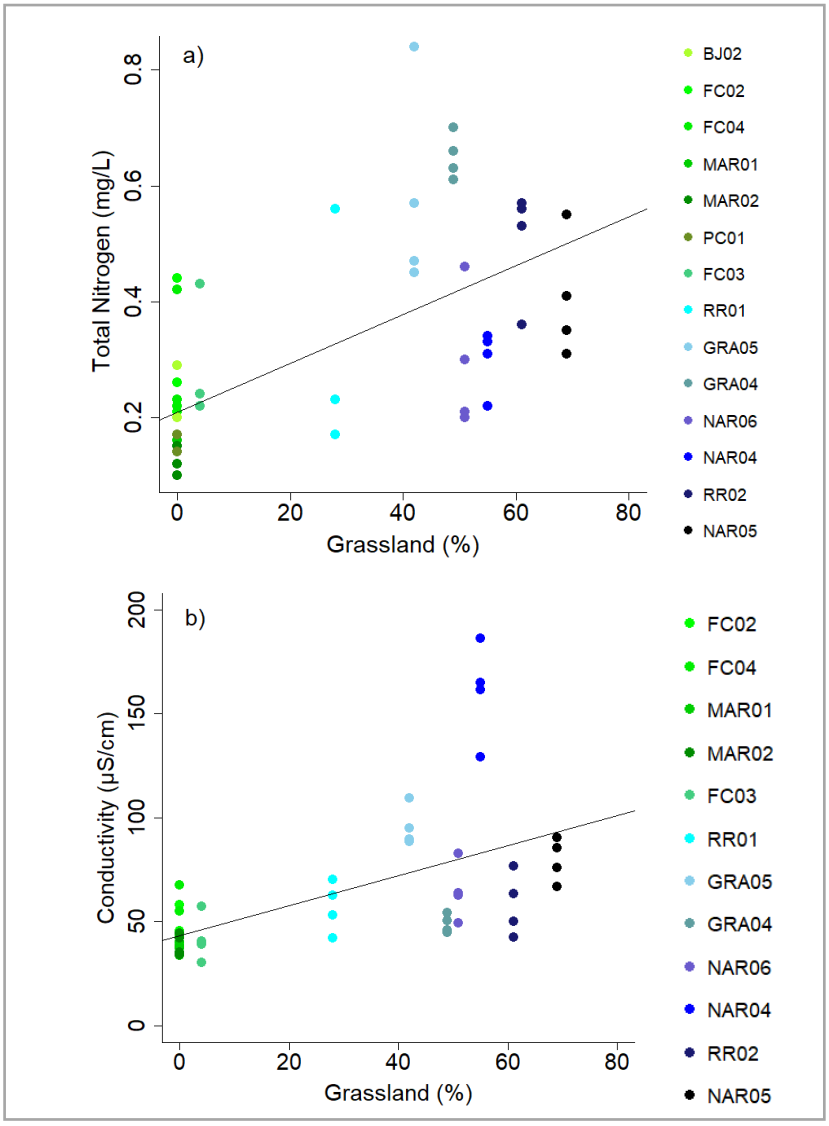

Figure 3.5: a) Total nitrogen in relation to grassland (%) for 14 headwater streams monitored monthly July-October 2016; **b)** Electrical conductivity in relation to grassland (%) for 12 headwater streams monitored monthly July-October 2016 (values overlap for forested sites). **Sites included:** Benjie's Lake Brook (BJ02) (for total nitrogen only), Fishing Cove River streams (FC02, FC03, FC04), Grande Anse River streams (GRA04, GRA05), Margaree River streams (MAR01, MAR02), North Aspy River streams (NAR04, NAR05, NAR06), Philip's Cove Brook (PC01) (for total nitrogen only), and Red River streams (RR01, RR02).

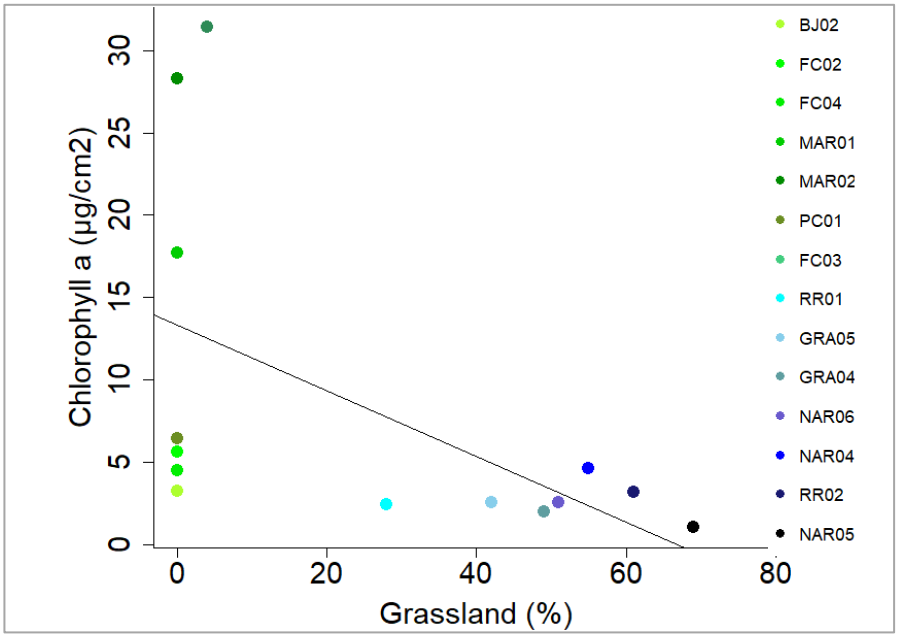

Figure 3.6: Chlorophyll *a* in relation to grassland (%) for 14 headwater streams collected after 5 weeks of colonization.

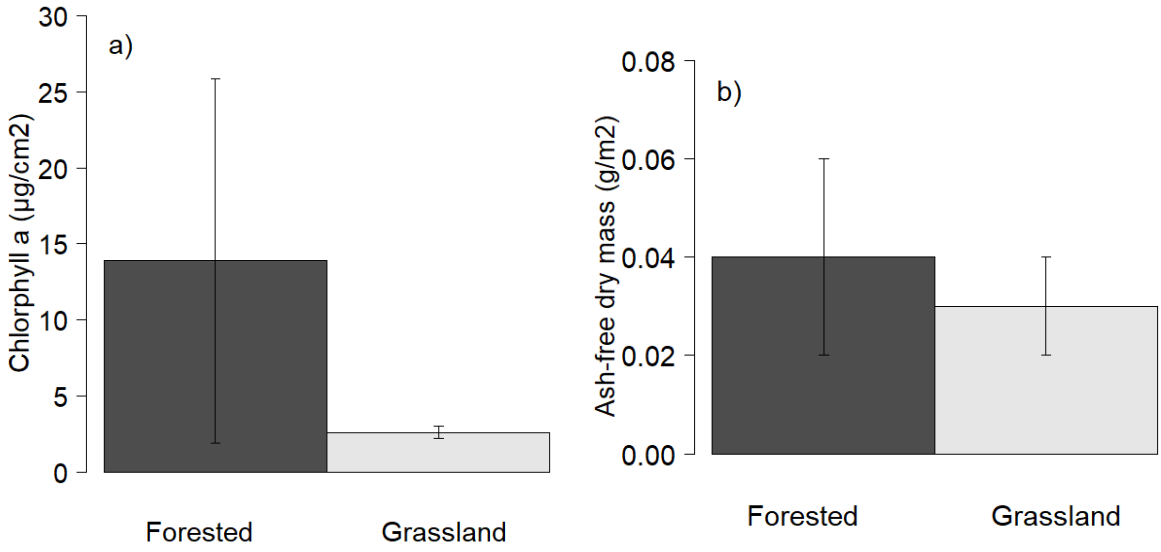

Figure 3.7: Average periphyton biomass for seven forested and seven grassland stream habitats, measured as a) chlorophyll *a* and b) ash-free dry mass. Bars represent means and error bars represent standard deviations of the data. Forested sites have a percentage of grassland range between 0-4 %, while grassland sites range between 28-69%.

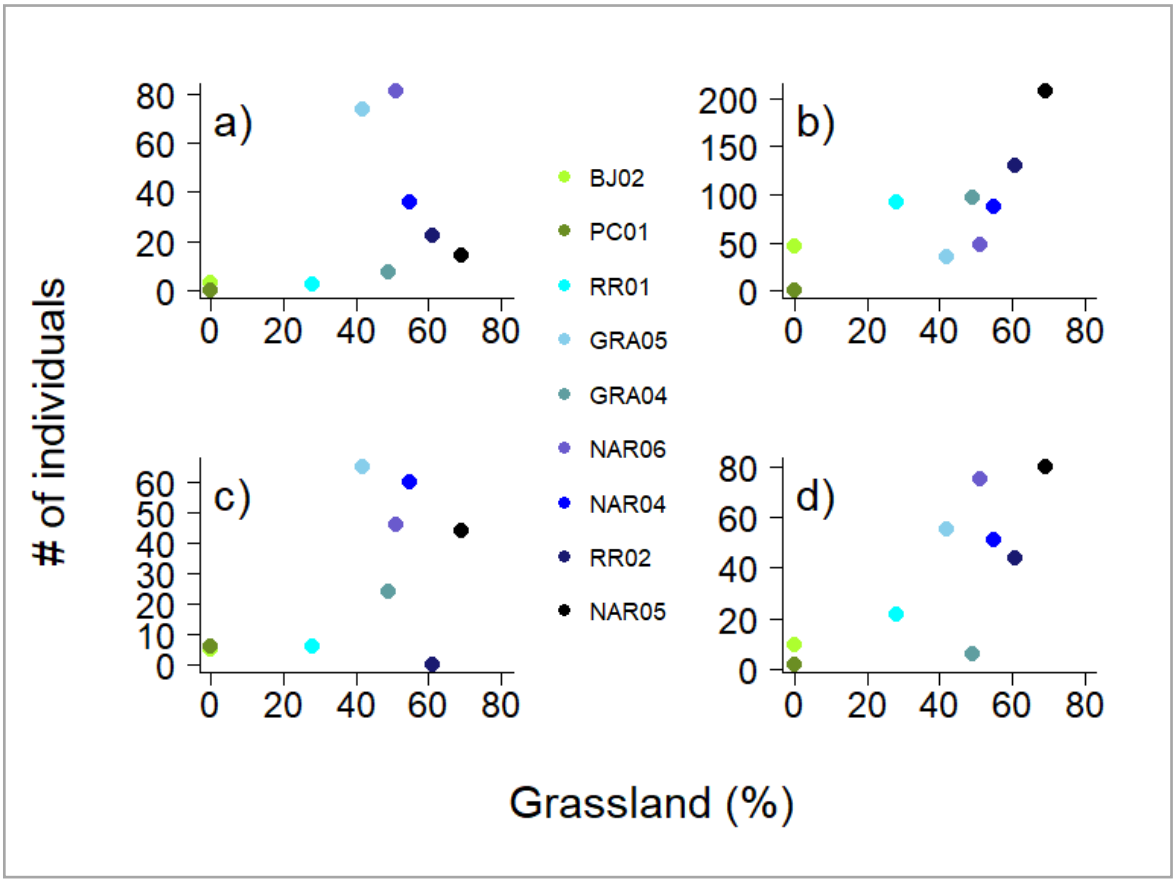

Figure 3.8: Total number of individuals for a) Baetidae, b) Ephemerellidae, c) Capniidae, and d) Philopotamidae families in relation to grassland for 9 headwater streams sampled October 2016. **Sites included:** Benjie's Lake Brook (BJ02), Grande Anse River streams (GRA04, GRA05), North Aspy River streams (NAR04, NAR05, NAR06), Philip's Cove Brook (PC01), and Red River streams (RR01, RR02).

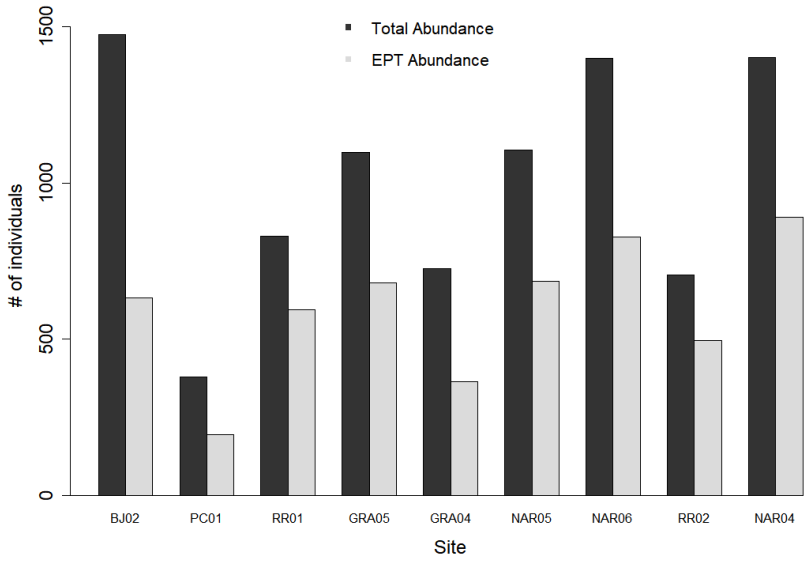

Figure 3.9: Total abundance and EPT abundance for 9 headwater streams sampled October 2016. Sites are ordered (left to right) from lowest to highest grassland percentage.

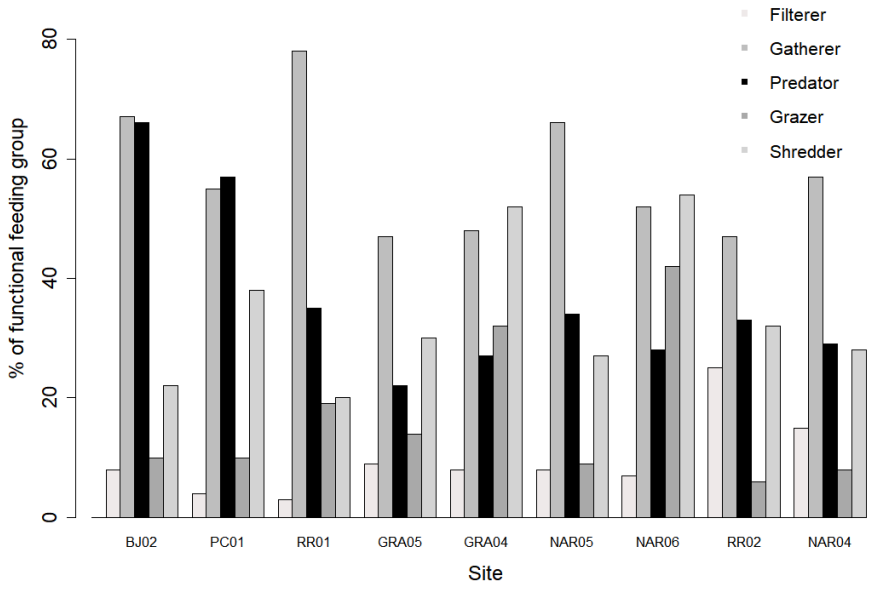

Figure 3.10: Percentage of functional feeding groups for 9 headwater streams sampled October 2016. Sites are ordered (left to right) from lowest to highest grassland percentage.

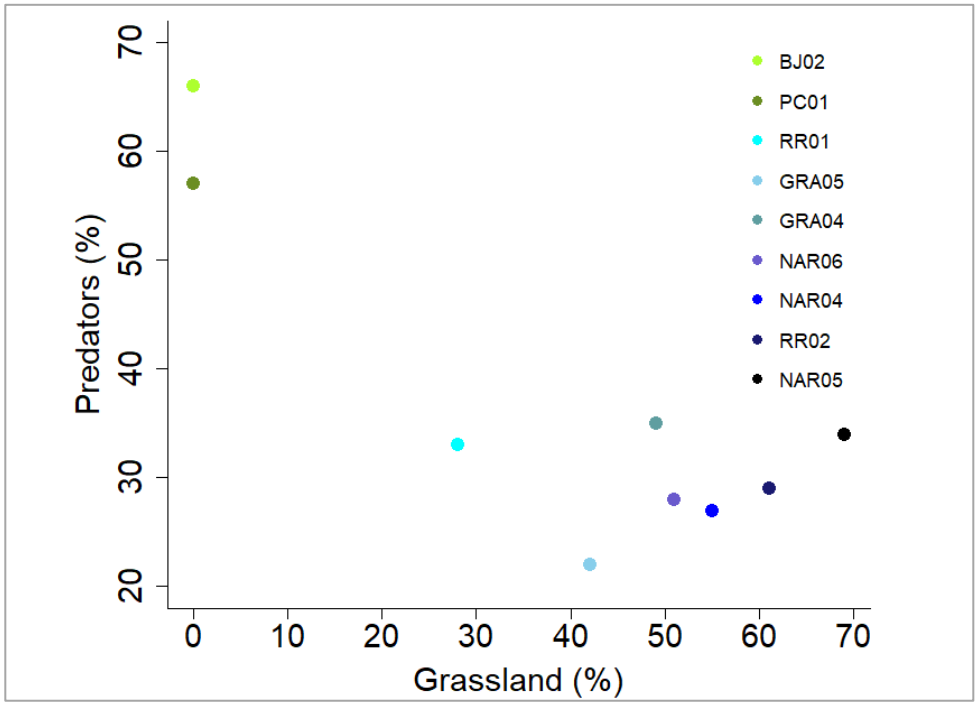

Figure 3.11: Predatory macroinvertebrate abundance in relation to grassland for 9 headwater streams sampled October 2016. **Sites included:** Benjie's Lake Brook (BJ02), Grande Anse River streams (GRA04, GRA05), North Aspy River streams (NAR04, NAR05, NAR06), Philip's Cove Brook (PC01), and Red River streams (RR01, RR02).

Table 3.1: AIC Model Selection for grassland effects on average daily maximum temperature, average temperature, maximum temperature, minimum temperature, and average daily range temperature for 13 headwater streams monitored July-September 2016. I show results for all models with $\Delta AIC_c < 8$.

Response	Model description	k	LL	AIC_C	ΔAIC_C	$\omega\ AIC_C$	R^2
ADM Stream Temperature (˚C)	Intercept	2	-20.26	45.73	0	0.55	-
	Grassland	3	-19.02	46.71	0.98	0.33	0.17
Average Stream Temperature (˚C)	Intercept	2	-15.78	36.76	0.00	0.74	-
	Grassland	3	-15.50	36.76	2.91	0.97	0.04
Maximum Stream Temperature (˚C)	Intercept	2	-27.27	59.74	0.00	0.64	-
	Grassland	3	-26.35	61.36	1.62	0.28	0.13
Minimum Stream Temperature (˚C)	Intercept	2	-10.38	25.96	0.00	0.76	-
	Grassland	3	-10.38	29.42	3.46	0.15	0.001
Average Daily Temperature Range (˚C)	Grassland	3	-14.34	37.35	0.00	0.67	0.34
	Intercept	2	-17.04	39.27	1.92	0.92	-

k, number of parameters; LL, log-likelihood; AICc, Akaike information criterion, ΔAICc, difference in AIC between most parsimonious model and subsequent models, $\omega\ AIC_C$, model weight.

Table 3.2: AIC Model Selection for grassland effects on total nitrogen and conductivity in headwater streams monitored monthly July-October. I show results for all models with $\Delta AIC_c < 8$.

	Model description	**k**	**LL**	**ΔAIC_C**	**ω AIC_C**	**Marginal R2**	**Conditional R2**
Total Nitrogen (mg/L)	Grassland + (1|Site) + Alders	5	42.29	0.00	1.00	0.67	0.69
	Intercept	2	31.47	19.30	0.00	-	-
Conductivity (µS/cm)	Grassland + (1|Site)	4	-205.85	0.00	0.77	0.31	0.88
	Intercept	3	-208.26	2.44	0.23	-	-

k, number of parameters; LL, log-likelihood; ΔAICc, difference in AIC between most parsimonious model and subsequent models, ω AIC_C, model weight; Marginal R^2, amount of variation explained by fixed effects; Conditional R^2; amount of variation explained by both fixed and random effects.

Table 3.3: AIC Model Selection for grassland effects on periphyton biomass measured as chlorophyll *a* and ash-free dry mass (AFDM) in 14 headwater streams. I show results for all models with $\Delta AIC_c < 8$.

	Model description	**k**	**LL**	**AIC_C**	**ΔAIC_C**	**ω AIC_C**	**R^2**
Chlorophyll *a* (µg/cm^2)	Grassland	3	-49.28	106.96	0.00	0.47	0.28
	Intercept	2	-51.63	108.34	1.39	0.23	-
	Grassland + Substrate Size	4	-48.26	108.97	2.01	0.17	0.38
	Grassland + Discharge	4	-48.95	110.34	3.39	0.09	0.32
	Grassland + Substrate Size + Discharge	5	-47.12	111.73	4.78	0.04	0.47
Ash-free dry mass (g/m^2)	Intercept	2	70.53	-135.97	0.00	0.43	-
	Grassland	3	71.86	-135.32	0.64	0.31	0.17
	Grassland + Substrate Size	4	73.14	-133.83	2.14	0.15	0.31
	Grassland + Discharge	4	75.11	-132.73	3.24	0.08	0.24
	Grassland + Substrate Size + Discharge	5	72.46	-132.48	3.48	0.03	0.48

k, number of parameters; LL, log-likelihood; ΔAICc, difference in AIC between most parsimonious model and subsequent models, ω AIC_C, model weight.

Table 3.4: AIC model selection for determining effects of grassland on family level taxa, total abundance, EPT abundance, and predatory macroinvertebrates in 9 headwater streams sampled October 2016. I show results for all models with $\Delta AIC_c < 8$.

	Model description	**k**	**LL**	**AICc**	**ΔAIC_c**	**D^2**
Baetidae	Grassland + Discharge	4	-62.48	70.48	0.00	0.75
	Grassland	3	-71.68	77.68	7.19	0.33
Ephemerellidae	Grassland	3	-92.94	98.94	0.00	0.36
	Grassland + Discharge	4	-91.93	99.93	0.99	0.42
	Intercept	2	-97.45	101.45	2.51	-
Capniidae	Grassland	3	-75.25	81.25	0.00	0.25
	Intercept	2	-78.25	82.25	1.00	-
Philopotamide	Grassland + Discharge	4	-70.87	78.87	0.00	0.74
	Grassland + Discharge + Dominant Tree Species	8	-65.78	79.78	0.91	0.85
	Grassland	3	-75.86	81.86	2.99	0.56
	Grassland + Dominant Tree Species	7	-72.94	84.94	6.07	0.68
Total Abundance (# of individuals)	Grassland + Dominant Tree Species	7	-117.48	129.48	0.00	0.80
	Grassland + Dominant Tree Species + Substrate Size	8	-115.88	129.88	0.40	0.83
	Intercept	2	-131.94	135.94	6.46	-
EPT Abundance (# of individuals)	Grassland + Dominant Tree Species	7	-105.98	117.98	0.00	0.85
	Intercept	2	-123.09	127.10	9.99	-
Shredders (%)	Grassland + Dominant Tree Species + Discharge	8	-58.06	72.06	0.00	0.68

	Intercept	2	-68.78	72.23	0.18	-
	Grassland + Discharge	4	-65.78	73.78	1.73	0.24
	Grassland + Dominant Tree Species	7	-61.82	73.82	1.76	0.52
	Grassland + Dominant Tree Species + Discharge + Substrate Size	8	-57.81	73.81	1.75	
	Grassland	3	-67.99	73.99	1.94	0.03
	Grassland + Dominant Tree Species + Substrate Size	8	-61.33	75.33	3.27	0.54
	Grassland + Substrate Size + Discharge	5	-65.68	75.68	3.63	0.25
	Grassland + Substrate Size	4	-67.98	75.99	3.93	0.02
Grazers (%)	Intercept	2	-65.50	69.50	0.00	-
	Grassland	3	-63.97	69.98	0.50	0.15
	Grassland + Dominant Tree Species	7	-63.05	75.05	5.55	0.24
Predators (%)	Grassland	3	-60.22	66.22	0.00	0.70
	Grassland + Substrate Size	4	-58.73	66.74	0.52	0.75
	Intercept	2	-70.79	74.79	8.58	-
Gatherers (%)	Grassland + Discharge	4	-61.75	69.75	0.00	0.43
	Intercept	2	-66.76	70.76	1.00	-
	Grassland	2	-66.75	72.75	3.00	0.0004
Filterers (%)	Grassland + Discharge	4	-48.37	56.34	0.00	0.54
	Intercept	2	-55.02	59.02	2.65	-
	Grassland + Discharge + Dominant Tree Species	8	-46.11	60.11	3.75	0.65
	Grassland	3	-54.99	60.99	4.63	0.003
	Grassland +Dominant Tree	7	-50.31	62.31	5.94	0.41

	Species					

k, number of parameters; LL, log-likelihood; AICc, Akaike information criterion, ΔAICc, difference in AIC between most parsimonious model and subsequent models, ω $AIC_{C,}$ model weigh; D^2, deviance explained.

CHAPTER 4: Conclusions

4.1 Significance of Study

There has been considerable work studying the connections between streams and riparian forests (see recent meta-analysis in Allen and Wesner 2016), as well as the effects of terrestrial ungulates on altering dynamics and productivity of boreal forest ecosystems (Pastor and Naiman 1992, McInnes et al. 1992, Kielland and Bryant 1998). Riparian forest and stream ecosystems are connected through flows of nutrients, energy, and organisms (Baxter et al. 2005). Thus, ecologists and land managers need to consider how moose mediated landscape changes can impact adjacent stream ecosystems. My thesis is one of the first investigations of terrestrial ungulate impacts on streams in the boreal forest ecosystem. Additionally, this study offers insight into cascading impacts of terrestrial consumers on aquatic consumers, such as macroinvertebrates. Flows of energy and organisms can exert strong influences on downstream ecological communities (Vannote et al. 1980). The knowledge gained will prove a valuable tool in assisting future stream restoration and moose management projects for Cape Breton Highlands National Park, as well as other areas of moose hyperabundance such as Terra Nova National Park in Newfoundland and Isle Royal National Park in Michigan.

4.2 Thesis Synopsis

Moose are drivers of landscape change in the boreal forest ecosystem and these changes can have repercussions on the adjoining network of streams and lakes. Large ungulates such as moose can over-browse favoured tree species such as balsam fir and white birch,

eventually increasing tree mortality and causing landscape pattern changes (McInnes et al. 1992, McLaren et al. 2009, Smith et al. 2010). These changes can be intensified in areas where episodic disturbances have occurred, as is the case in the Cape Breton Highlands, Nova Scotia. During the 1970s and 80s, a spruce budworm outbreak killed ~90% of the mature boreal forest coniferous stands (Ostaff and MacLean 1989). Balsam fir with some deciduous tree saplings began to regenerate, which created an abundant food source for moose (Parks Canada 2015). Low levels of predation and disease coupled with increased food supply allowed moose to reach hyperabundance and thus changed the direction of forest regeneration (Smith 2007, Parks Canada 2015). Many areas within CBHNP were not able to regenerate due to moose hyperabundance and now ~11% of the landscape is grassland dominated (Parks Canada 2015). The nature of ungulate herbivory-spruce budworm disturbance has been thoroughly investigated; however, effects of moose hyperabundance on adjacent stream ecosystems has been largely overlooked.

It has long been recognized that the surrounding terrestrial ecosystem has major influence on the structure and function of stream ecosystems (Vannote et al. 1980). Changes in riparian vegetation via forest harvesting increases stream temperatures (Sweeney 1993, Johnson and Jones 2000, Gomi et al. 2006), nutrients, and conductivity (Richardson and Beraud 2014), stream periphyton communities (Kiffney et al. 2003, Wilkerson et al. 2010), and alters macroinvertebrate community structure (Sweeney 1993, Danehy et al. 2007, Wilkerson et al. 2010). I used this knowledge to develop predictions about the effects of hyperabundant moose on mid-order (Chapter 2) and first-order (Chapter 3) streams, using both long-term data (2005-2014) and a field study (2016)

within the Cape Breton Highlands. ArcGIS was employed using Parks Canada (Chapter 2) and NSDNR (Chapter 3) land classification layers to determine the level of moose mediated grasslands in each of the studies' watersheds. I predicted that streams with higher levels of grasslands in their watersheds will have i) higher stream temperatures; ii) higher total nitrogen and conductivity, iii) higher periphyton biomass (Chapter 3 only), and iv) higher total and EPT abundances, with altered macroinvertebrate community structure.

In Chapter 2, I analyzed data collected by Parks Canada on stream temperature, total nitrogen, conductivity, and macroinvertebrates in relation to the percentage of moose impacted landscape (includes grasses, ferns and open areas) in the watershed. I found no evidence to support my predictions that watersheds with higher levels of moose impacts have higher stream temperatures, higher total/EPT abundances, and altered macroinvertebrate assemblages. However, I did found evidence to support my predictions that watersheds with higher levels of moose impacts have higher levels of total nitrogen and conductivity. These results potentially demonstrate that loss of tree biomass upland of study streams is reducing interception and increasing the transport of dissolved nutrients to streams (Keenan and van Dijk 2010). Grassland dominated riparian buffer zones have less retention and higher nitrogen mobilization than forest dominated buffers (Simmons et al. 1992, Lee et al. 2004). Therefore, the decreased ability of grass-dominated riparian zones to retain nutrients and the increase in open areas are perhaps responsible for the increase in total nitrogen. Increased conductivity in areas with elevated moose impacts further suggests that surface runoff is more significant and ion-contributing materials are

more available due to disturbed soils or reduced organic horizons exposing mineral layers (Wenger 1984).

In Chapter 3, I conducted a field study to compare headwater streams that flow throughout the grassland habitat on the plateau of North Mountain in CBHNP to similar streams found in areas predominately surrounded by mature boreal forest. I found that moose-mediated grassland streams had higher average daily temperature ranges than forested streams. The suspected decrease in shading of grassland streams relative to forested streams due to reduced canopy cover may be contributing to greater diel fluctuations. As observed in Chapter 2, I found evidence to support the prediction that streams with higher moose mediated grasslands have higher total nitrogen and conductivity. As discussed above for Chapter 2, this could be because grasslands sites have fewer trees and more open areas that can reduce rainfall interception and facilitate greater surface runoff (Jakob and Hungr 2005). However, current forest data from NSDNR suggests that the presence and abundance of nitrogen-fixing alders may also influence total nitrogen levels. I found evidence that the stream invertebrate families Baetidae, Ephemerellidae, Capniidae, and Philopotamide have higher abundances in the moose mediated grassland streams than the forested streams. However, likewise to Chapter 2, I found no evidence that total/EPT macroinvertebrate abundances and macroinvertebrate community structure were influenced by grasslands. Although, I found changes in streamside plant communities' due to hyperabundant moose effects may be increasing habitat heterogeneity thereby increasing these specific taxa.

Overall, my analyses of long-term data (2005-2014) of mid-order streams and a field study data (2016) for first order streams demonstrate the moose impacted landscape of North Mountain is influencing nutrients and dissolved ions entering streams. Stream temperature of larger riverine systems are less influenced by riparian shade, as headwaters typically have closed canopies with a greater connection to the surrounding landscape (Richardson and Danehy 2007). Thus, I would expect headwaters to be more influenced by the loss of treed habitat than mid-ordered streams and lack of evidence in Chapter 2 for changes in macroinvertebrate community structure is not surprising. In Chapter 3, higher abundances of specific macroinvertebrate taxa were attributed to greater numbers of grasses and alder shrubs in relation to conifer-dominated streams. These alders are typical of headwater streams, however, the level on the disturbed landscape of North Mountain has been increasing (Sean Basquill, Provincial Biologist, NSDNR, *personal communication*). The absence of conifers and the advancement of alders is expected to facilitate greater macroinvertebrate abundances transported downstream to fish-bearing habitats.

4.3 Research Perspectives

To my knowledge, this is the first study to investigate terrestrial ungulate impacts on stream ecosystems (but see Bakker et al. 2016, Bump et al. 2009, 2017). I found evidence that intense moose herbivory can cross ecosystem boundaries impacting nutrients and dissolved ions in streams at two scales of inquiry, however, there remains considerable residual variation in most of my analyses. Therefore, I believe the following factors may help explain moose impacts on streams: i) measuring soil nitrogen, ii) experimental set-

ups measuring nitrogen inputs, iii) exclosures around or near streams measuring riparian vegetation, and iv) higher resolution land cover data or more field surveys on wetland vegetation.

To confirm that streams with higher levels of moose impacted landscapes contained higher levels of total nitrogen, I proposed future stream research in CBHNP concentrate their efforts on streamside and in-stream nitrogen concentrations. The disturbed landscape of North Mountain not only contains high amounts of grasses, but also alders. Research shows higher levels of nitrogen-fixing alders in disturbed landscapes increase soil nitrogen concentrations and cycling rates (Binkley et al. 1992). Measuring nitrogen mineralization and nitrification rates at sites with differing levels of moose impacted landscapes may help determine if changes in streamside plant communities are influencing soil nitrogen. Additionally, moose defecation may be playing a role in nutrient inputs into nearby stream ecosystems. As noted by Persson et al. (2000), moose supply a considerable amount of soil nitrogen in the form of urine and feces that may affect fungi and invertebrate communities. Research looking at the effects of introduced cow manure on macroinvertebrate functional feeding groups found that manure was utilized by all functional feeding groups and increased the abundance of specific taxa (De Rosario et al. 2002). Therefore, it is conceivable that runoff from moose feces could support higher abundances of macroinvertebrates due to nutrient enrichment. Future research on moose effects on nutrient inputs in streams should involve experimental set-ups under precisely controlled inputs of moose feces to determine effects on stream biota. Additionally, these experiments may prove useful in determining

the level of nitrogen retention by riparian vegetation with differing plant species communities.

Future long-term research on plant species communities in the disturbed habitat of North Mountain may consider placing exclosures around stream environments. High levels of alders in these streams could be outcompeting the highly browsed conifer saplings. Exclosures around moose mediated grassland streams could determine if conifers outcompete alders in these habitats and whether they can thrive in areas with prominent grassland. Additionally, accurate data on plant communities such as shrubs and ferns that are overtaking the disturbed landscape are of outmost importance. Currently, there is inaccurate data on the number of speckled alders in all headwater streams monitored. This may have attributed to errors in land cover classification due to edge effects that are common for smaller wetlands found in the headwater streams (Frances MacKinnon, Wildlife GIS analyst, NSDNR*, personal communication*). Thus, more field surveys or higher resolution images are recommended for small wetland vegetation classification. Field studies measuring the size and abundance of alders would be useful in determining true densities of these shrubs and how they may be altered by hyperabundant moose.

4.4 Management Implications

The restoration of the boreal forest is of utmost importance to Cape Breton Highlands National Park and park managers have taken some steps to facilitate the regeneration of the boreal forest region. In partnership with the Mi'kmaq community, the moose management team has established a moose reduction program to effectively reduce the

browsing pressure of hyperabundant moose on North Mountain (Parks Canada 2015). In the past two years, 87 moose have been removed and preliminary work suggests that there is a reduction in browse damage (Clayton D'Orsay, Conservation Officer II, Parks Canada, *personal communication*). Although the localized release of browsing pressure is positive, continued monitoring is necessary to accurately assess the impact of the controlled hunt. In addition, areas with high levels of grassland are speculated to exist for some time with long-term consequences for the both terrestrial and aquatic ecosystems. Therefore, I recommend the following be considered by Parks Canada's Bring Back the Boreal Project:

- Parks Canada's water quality and benthic macroinvertebrate program should increase the number of sites located in moose impacted regions of CBHNP, specifically including more 1st and 2nd order streams in their monitoring program.
- In the event of another spruce budworm outbreak it is recommended that annual monitoring be continued in those streams that will most likely be affected (*i.e.* mature to old-growth boreal forest stands) to account for any changes in stream ecosystem variables as identified in this study.
- Moose browse transects established adjacent to streams throughout North Mountain may provide useful information about how moose utilize various aspects of the boreal forest habitat in relation to upland areas where over-browsed trees and grasslands dominate the landscape.
- Moose exclosures near or around stream ecosystems would provide useful information about the persistence of alders or their effect on stream biota. Alders

may be outcompeting conifer seedlings and browsed saplings in the riparian habitat. Thus, exclosures could inform us if removal of alders and forest restoration by planting trees via streamside is warranted.

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Appendix A - Additional data and results for Chapter 2

Table A1: Parks Canada stream monitoring sites, showing included or excluded based on limitations for stream temperature, total nitrogen, conductivity, and macroinvertebrate analysis.

No.	Site ID	Name	Years Sampled for stream temperature	Years sampled for water chemistry & invertebrates	Area of Watershed (km^2)	Included/Excluded in Analysis	Limitations
1	AB01	Aucoin's Brook	2006	2006, 2008	5.64	Excluded	Bridge
2	AB02	Aucoin's Brook	0	2008	3.64	Excluded	Bridge
3	BJ01	Benjie's Brook	2007, 2008, 2009, 2014, 2015, 2016	2006-2016	6.16	Included	n/a
4	BLA01	MaryAnn Brook	0	2005, 2009, 2013	21.05	Excluded	Overlapping BLA03
5	BLA02	Black Brook	2005	2005	85.04	Excluded	Exceeds set limit of $65km^2$
6	BLA03	Branch Pond Inlet	2007- 2016	2007- 2016	5.69	Included	n/a
7	BPC1	Beaver Pond Creek	0	2007	0.61	Excluded	Salt shed
8	BPC2	Beaver Pond Creek	0	2007	0.66	Excluded	Salt shed
9	BPC3	Beaver Pond Creek	0	2007	0.68	Excluded	Salt shed
10	CB01	Canadian Brook	0	2009	1.47	Included	n/a
11	CHE01	Roberts Brook	2006-2014	2005. 2006 2011, 2014	27.09	Included	n/a
12	CHE02	Cheticamp River	0	2005	236.61	Excluded	Exceeds set limit of $65km^2$
13	CHE03	Daphine Brook	2006	2005	5.73	Included	n/a
14	CHE04	Cheticamp Lake	2007-2015	2007-2014	50.32	Excluded	Dam
15	CLY01	Clyburn Brook	2004-2016	2005, 2008-2016	65.09	Included	n/a
16	CLY02	State Brook	0	2005	2.52	Excluded	Overlapping CLY01
17	CLY03	Soapstone Brook	0	2005	21.52	Excluded	Overlapping CLY01
18	COR01	Corney Brook	2006- 2016	2006- 2016	25.06	Included	n/a
19	DUN01	Dundas Brook	2007- 2016	2006- 2016	29.94	Included	n/a
20	EFF01	Effie's	2007- 2016	2006- 2016	14.92	Included	n/a

		Brook					
21	FIS	Fiset Brook	2005, 2006	0	20.22	Included in temp only	n/a
22	FC01	Fishing Cove River	0	2006	6.24	Included	n/a
23	GA-1	Grande Anse River	2014	0	50.84	Included in temp only	n/a
24	GB01	Glasgow Brook	0	2006	8.99	Included	n/a
25	GRA	Grande Anse River	2006	0	30.62	Included in temp only	n/a
26	GRA01	Grande Anse River	0	2006	17.66	Included	n/a
27	GRA02	GrandeAnse River	0	2005	1.67	Included	n/a
28	GRA03	MacIntosh Brook	0	2005	8.77	Included	n/a
29	JB01	Jumping Brook	0	2008	3.37	Included	n/a
30	LS01	Little Smokey Stream	0	2005	0.17	Excluded	Too small (<1km^2)
31	MAC01	MacKenzie River	0	2008	73.06	Excluded	Exceeds set limit of 65km^2
32	MAR01	Marrach Stream	0	2005, 2007, 2008	1.31	Excluded	Abandoned campground/landfill
33	MAR02	Marrach Stream	0	2005, 2007, 2008, 2010	1.37	Excluded	Abandoned campground/landfill
34	MAR03	Marrach Stream	0	2005, 2008	1.40	Excluded	Abandoned campground/landfill
35	NAR01	McGregor Brook	0	2005	3.78	Included	n/a
36	NAR02	Little Southwest Brook	0	2005, 2007	12.19	Included	n/a
37	NAR03	North Aspy River	2005	2005, 2006, 2007, 2011, 2012	85.09	Excluded	Exceeds set limit of 65km^2
38	NB01	Neil Brook	0	2005	13.54	Included	n/a
39	SAR01	South Aspy River	0	2006	16.86	Included	n/a
40	SB01	Still Brook	2007-2015	2007-2016	3.34	Included	n/a
41	TBC01	Trout Brook (Aucoin's)	0	2006	4.66	Excluded	Sampled in November
42	TRB01	Trout Brook	0	2006	4.47	Excluded	Sampled in November
43	WB01	Warren Brook	0	2005, 2009, 2013, 2016	33.67	Included	n/a

Table A2: Stream temperature parameters and predictor variables for 12 sites monitored during summer 2006-2016.

Site	Year	Average Maximum Daily Stream Temperature (°C)	Average Stream Temperature (°C)	Maximum Stream Temperature (°C)	Average Maximum Daily Air Temperature (°C)	Average Air Temperature (°C)	Maximum Air Temperature (°C)	Grassland (%)	Slope (m/m)	Stream Order
BJ01	2008	17.93	15.91	23.98	20.14	16.62	29.50	8	0.07	3
BJ01	2009	17.30	14.95	22.57	18.86	14.97	26.50	8	0.07	3
BJ01	2011	16.06	14.35	20.34	18.64	14.40	26.80	8	0.07	3
BJ01	2012	17.63	15.92	21.73	21.09	16.81	27.00	8	0.07	3
BJ01	2013	17.04	15.32	21.43	20.54	15.96	28.60	8	0.07	3
BJ01	2014	17.51	15.78	22.47	20.66	16.31	29.10	8	0.07	3
BLA03	2007	18.44	16.01	25.90	22.85	17.51	32.50	6	0.07	3
BLA03	2008	18.22	16.10	25.10	22.72	18.03	31.80	6	0.07	3
BLA03	2009	18.31	15.87	24.87	21.97	17.03	32.80	6	0.07	3
BLA03	2010	18.01	16.15	24.84	22.85	17.96	32.60	6	0.07	3
BLA03	2011	17.60	15.20	22.85	21.30	16.61	29.90	6	0.07	3
BLA03	2012	19.46	16.91	24.94	23.43	18.65	32.00	6	0.07	3
BLA03	2013	19.26	16.90	25.09	23.75	18.19	33.30	6	0.07	3
BLA03	2014	19.35	17.08	25.23	23.68	18.22	33.10	6	0.07	3

BLA03	2015	18.27	15.99	24.49	22.01	17.21	32.80	6	0.07	3
CHE01	2006	14.73	13.72	19.68	22.60	18.39	30.80	17	0.25	3
CHE01	2008	14.16	12.52	18.32	23.03	18.48	31.90	17	0.25	3
CHE01	2009	14.48	13.60	18.60	22.66	17.81	30.60	17	0.25	3
CHE01	2010	14.65	13.76	18.30	23.13	18.43	31.40	17	0.25	3
CHE01	2011	13.69	14.02	17.9	22.05	17.35	29.90	17	0.25	3
CHE01	2012	15.37	13.12	18.23	24.11	19.12	30.60	17	0.25	3
CHE01	2013	14.66	14.59	17.89	23.18	18.10	31.50	17	0.25	3
CHE01	2014	14.80	14.02	17.89	23.17	18.11	31.50	17	0.25	3
CHE03	2006	15.07	14.02	19.68	22.60	18.39	30.80	7	0.18	3
CLY01	2006	18.07	14.26	19.4	24.14	17.82	31.90	7	0.20	5
CLY01	2007	17.65	16.36	22.70	22.85	17.51	32.50	7	0.20	5
CLY01	2009	17.22	15.72	23.28	21.97	17.03	32.80	7	0.20	5
CLY01	2010	18.55	15.15	24.27	22.85	17.96	32.60	7	0.20	5
CLY01	2011	16.70	16.25	20.48	21.30	16.61	29.90	7	0.20	5
CLY01	2012	18.40	14.79	22.63	23.43	18.65	32.00	7	0.20	5
CLY01	2014	18.44	16.44	22.49	23.68	18.22	33.10	7	0.20	5
CLY01	2015	17.30	15.28	21.99	22.01	17.21	32.80	7	0.20	5

CLY01	2016	18.66	16.45	23.21	23.02	17.82	31.40	7	0.20	5
COR01	2006	15.71	16.61	21.4	22.60	18.39	30.80	10	0.18	4
COR01	2009	15.91	14.52	21.40	22.66	17.81	30.60	10	0.18	4
COR01	2012	17.70	14.67	21.7	24.11	19.12	30.60	10	0.18	4
COR01	2014	16.96	16.05	21.99	23.17	18.11	31.50	10	0.18	4
COR01	2015	15.71	14.55	21.15	22.25	17.53	29.20	10	0.18	4
COR01	2016	16.62	15.26	19.87	22.13	17.62	28.40	10	0.18	4
DUN01	2007	16.65	15.54	23.60	22.85	17.51	32.50	7	0.18	3
DUN01	2009	16.05	14.99	22.41	21.97	17.03	32.80	7	0.18	3
DUN01	2014	17.93	14.54	23.26	23.68	18.22	33.10	7	0.18	3
DUN01	2016	17.38	15.39	24.002	23.02	17.82	31.40	7	0.18	3
EFF01	2007	17.33	16.10	24.90	22.85	17.51	32.50	8	0.14	3
EFF01	2008	17.02	15.84	23.70	22.72	18.03	31.80	8	0.14	3
EFF01	2009	15.60	15.80	22.54	21.97	17.03	32.80	8	0.14	3
EFF01	2010	17.85	14.22	24.38	22.85	17.96	32.60	8	0.14	3
EFF01	2011	15.95	16.39	21.3	21.30	16.61	29.90	8	0.14	3
EFF01	2012	18.33	14.73	22.97	23.43	18.65	32.00	8	0.14	3
EFF01	2013	18.30	16.82	23.23	23.75	18.19	33.30	8	0.14	3

EFF01	2014	18.57	16.69	24.97	23.68	18.22	33.10	8	0.14	3
EFF01	2015	16.84	15.66	21.92	22.01	17.21	32.80	8	0.14	3
EFF01	2016	17.26	16.15	20.77	23.02	17.82	31.40	8	0.14	3
FIS	2006	15.89	17.14	21.9	22.60	18.39	30.80	5	0.09	3
GA1	2014	15.70	14.44	22.05	20.66	16.31	29.10	18	0.07	4
GRA	2006	10.52	14.03	23.2	19.70	15.95	22.90	24	0.06	4
SB01	2008	16.20	10.06	21.22	22.72	18.03	31.80	1	0.08	3
SB01	2009	15.75	15.17	21.75	21.97	17.03	32.80	1	0.08	3
SB01	2010	15.52	14.54	22.27	22.85	17.96	32.60	1	0.08	3
SB01	2011	14.90	16.88	19.32	21.30	16.61	29.90	1	0.08	3
SB01	2012	16.65	13.84	20.44	23.43	18.65	32.00	1	0.08	3
SB01	2013	16.74	15.38	20.79	23.75	18.19	33.30	1	0.08	3
SB01	2014	17.02	15.29	22.06	23.68	18.22	33.10	1	0.08	3
SB01	2015	16.73	14.73	26.45	22.01	17.21	32.80	1	0.08	3
SB01	2016	16.44	15.10	19.56	23.02	17.82	31.40	1	0.08	3

Table A3: Climate data for North Mountain, Ingonish, and Cheticamp weather stations showing average maximum daily, average, and maximum air temperatures for summer 2006-2016.

Station	Year	Average Maximum Daily Air Temperature (°C)	Average Air Temperature (°C)	Maximum Air Temperature (°C)
North	2006	19.70	15.95	22.90
Ingonish	2006	24.14	17.82	31.90
Cheticamp	2006	22.60	18.39	30.80
Ingonish	2007	22.85	17.51	32.50
North	2008	20.14	16.62	29.50
Ingonish	2008	22.72	18.03	31.80
Cheticamp	2008	23.03	18.48	31.90
North	2009	18.86	14.97	26.50
Ingonish	2009	21.97	17.03	32.80
Cheticamp	2009	22.66	17.81	30.60
North	2010	18.81	14.79	27.40
Ingonish	2010	22.85	17.96	32.60
Cheticamp	2010	23.13	18.43	31.40
North	2011	18.64	14.40	26.80
Ingonish	2011	21.30	16.61	29.90
Cheticamp	2011	22.05	17.35	29.90
North	2012	21.09	16.81	27.00
Ingonish	2012	23.43	18.65	32.00
Cheticamp	2012	24.11	19.12	30.60
North	2013	20.54	15.96	28.60
Ingonish	2013	23.75	18.19	33.30
Cheticamp	2013	23.18	18.10	31.50
North	2014	20.66	16.31	29.10
Ingonish	2014	23.68	18.22	33.10
Cheticamp	2014	23.17	18.11	31.50
Ingonish	2015	22.01	17.21	32.80
Cheticamp	2015	22.25	17.53	29.20
North	2016	19.87	15.48	29.00
Ingonish	2016	23.02	17.82	31.40
Cheticamp	2016	22.13	17.62	28.40

Table A4: Total nitrogen, specific conductivity, grassland, and environmental variables for 21 sites monitored during fall 2005-2014.

Site	Year	Total Nitrogen (mg/L)	Specific Conductivity (µS/cm)	Grassland (%)	Stream Order	Slope (m/m)	Elevation (m)	Area (km2)
BJ01	2006	0.21	54.9	8	3	0.07	315	6.16
BJ01	2007	0.2	41.4	8	3	0.07	315	6.16
BJ01	2008	0.06	40.8	8	3	0.07	315	6.16
BJ01	2009	0.23	42.8	8	3	0.07	315	6.16
BJ01	2010	0.27	40.1	8	3	0.07	315	6.16
BJ01	2011	0.24	49.9	8	3	0.07	315	6.16
BJ01	2012	0.2	41.4	8	3	0.07	315	6.16
BJ01	2013	0.35	41.9	8	3	0.07	315	6.16
BJ01	2014	0.2	42.4	8	3	0.07	315	6.16
BLA03	2007	0.27	40.8	6	3	0.07	385	5.69
BLA03	2008	0.17	26.2	6	3	0.07	385	5.69
BLA03	2009	0.26	38.3	6	3	0.07	385	5.69
BLA03	2010	0.26	27.4	6	3	0.07	385	5.69
BLA03	2011	0.2	30.6	6	3	0.07	385	5.69
BLA03	2012	0.19	36.8	6	3	0.07	385	5.69
BLA03	2013	0.29	40.2	6	3	0.07	385	5.69
BLA03	2014	0.18	29.3	6	3	0.07	385	5.69
CB01	2009	0.33	103.2	10	3	0.33	250	25.06
CHE01	2005	0.16	47.9	17	3	0.25	310	27.09
CHE01	2006	0.23	66.4	17	3	0.25	310	27.09
CHE01	2011	0.36	53.1	17	3	0.25	310	27.09
CHE01	2014	0.23	69	17	3	0.25	310	27.09
CHE03	2005	0.1	43.8	5	3	0.18	320	5.73
CLY01	2005	0.1	65.9	7	5	0.20	353	65.09
CLY01	2008	0.18	47	7	5	0.20	353	65.09
CLY01	2010	0.13	48.3	7	5	0.20	353	65.09
CLY01	2011	0.16	58.7	7	5	0.20	353	65.09
CLY01	2012	0.15	42.1	7	5	0.20	353	65.09
CLY01	2013	0.13	50.9	7	5	0.20	353	65.09
CLY01	2014	0.13	54.5	7	5	0.20	353	65.09
COR01	2005	0.09	52.6	10	4	0.18	321	25.06
COR01	2007	0.25	66.9	10	4	0.18	321	25.06
COR01	2008	0.2	62.4	10	4	0.18	321	25.06
COR01	2009	0.34	50.5	10	4	0.18	321	25.06
COR01	2010	0.33	53.6	10	4	0.18	321	25.06
COR01	2011	0.35	50.3	10	4	0.18	321	25.06
COR01	2012	0.28	59.2	10	4	0.18	321	25.06
COR01	2013	0.26	54.5	10	4	0.18	321	25.06
COR01	2014	0.27	51.6	10	4	0.18	321	25.06
DUN01	2006	0.22	54.7	7	3	0.18	340	29.94
DUN01	2007	0.18	46.5	7	3	0.18	340	29.94
DUN01	2008	0.18	40.5	7	3	0.18	340	29.94
DUN01	2009	0.28	44	7	3	0.18	340	29.94

DUN01	2010	0.17	34.9	7	3	0.18	340	29.94
DUN01	2011	0.14	49.1	7	3	0.18	340	29.94
DUN01	2012	0.15	35.2	7	3	0.18	340	29.94
DUN01	2013	0.1	44.9	7	3	0.18	340	29.94
DUN01	2014	0.14	44	7	3	0.18	340	29.94
EFF01	2005	0.11	76.2	8	3	0.14	275	14.92
EFF01	2007	0.22	56.4	8	3	0.14	275	14.92
EFF01	2008	0.1	61.3	8	3	0.14	275	14.92
EFF01	2009	0.27	59	8	3	0.14	275	14.92
EFF01	2010	0.18	52.7	8	3	0.14	275	14.92
EFF01	2011	0.14	67.7	8	3	0.14	275	14.92
EFF01	2012	0.19	42.3	8	3	0.14	275	14.92
EFF01	2013	0.23	47.9	8	3	0.14	275	14.92
EFF01	2014	0.13	56.1	8	3	0.14	275	14.92
FC01	2006	0.27	55.2	9	2	0.06	445	6.24
GB01	2006	0.17	47.8	11	2	0.13	348	8.99
GRA01	2005	0.21	82.6	28	3	0.22	306	17.66
GRA02	2005	0.24	113	36	3	0.22	288	1.67
GRA03	2005	0.17	88.2	15	3	0.21	310	8.77
GRA03	2009	0.26	70.5	15	3	0.21	310	8.77
GRA03	2012	0.17	61.7	15	3	0.36	310	8.77
JB01	2008	0.25	41.9	9	2	0.14	306	3.37
NAR01	2005	0.49	157	50	3	0.36	288	3.78
NAR02	2005	0.2	48	15	3	0.25	339	12.19
NAR02	2007	0.34	34	15	3	0.25	339	12.19
NB01	2006	0.27	97.7	7	2	0.08	208	13.54
SAR01	2006	0.31	186.7	15	2	0.14	344	16.86
SB01	2006	0.3	52.6	1	3	0.08	159	3.34
SB01	2007	0.27	47.8	1	3	0.08	159	3.34
SB01	2008	0.21	44.4	1	3	0.08	159	3.34
SB01	2009	0.2	45.3	1	3	0.08	159	3.34
SB01	2010	0.36	47.3	1	3	0.08	159	3.34
SB01	2011	0.22	45.9	1	3	0.08	159	3.34
SB01	2012	0.4	48.2	1	3	0.08	159	3.34
SB01	2013	0.36	53.1	1	3	0.08	159	3.34
SB01	2014	0.26	47.9	1	3	0.08	159	3.34
WB01	2005	0.15	34.5	6	3	0.04	208	33.67
WB01	2009	0.23	31.3	6	3	0.04	208	33.67
WB01	2011	0.17	27.45	6	3	0.04	208	33.67
WB01	2013	0.24	32	6	3	0.04	208	33.67

Table A5: Aquatic macroinvertebrate metrics, grassland, and environmental variables for 21 sites monitored during summer 2005-2014.

Site	Year	Filterers (%)	Gatherers (%)	Predators (%)	Grazers (%)	Shredders (%)	Total Abundance	EPT Abundance	Grassland (%)	Stream Order	Substrate Class Type (0-9)	Elevation (m)
BJ01	2006	2	74	69	17	8	3167	1122	8	3	6	315
BJ01	2007	4	46	39	35	16	2782	1991	8	3	6	315
BJ01	2008	3	20	23	56	20	376	336	8	3	7	315
BJ01	2009	5	24	25	40	27	937	766	8	3	7	315
BJ01	2010	6	19	16	65	18	954	873	8	3	6	315
BJ01	2011	5	76	81	12	5	8025	1900	8	3	8	315
BJ01	2012	4	53	39	31	18	3010	1870	8	3	7	315
BJ01	2013	8	40	31	45	20	4100	2988	8	3	7	315
BJ01	2014	15	27	32	33	26	2531	1908	8	3	6	315
BLA03	2007	4	67	28	42	30	1103	754	6	3	7	385
BLA03	2008	2	42	24	21	58	1982	1309	6	3	5	385
BLA03	2009	1	50	30	21	49	1655	1111	6	3	5	385
BLA03	2010	3	79	29	41	18	2443	1543	6	3	5	385
BLA03	2011	2	74	54	20	20	4628	2128	6	3	5	385
BLA03	2012	8	57	33	31	28	1308	872	6	3	5	385
BLA03	2013	5	62	30	33	36	4571	2900	6	3	5	385
BLA03	2014	3	70	30	38	28	2761	1600	6	3	6	385
CB01	2009	1	64	65	24	15	4300	2012	10	3	6	250
CHE01	2005	6	52	37	46	16	541	425	17	3	6	310
CHE01	2006	1	35	10	69	11	2346	2246	17	3	6	310
CHE01	2011	7	60	57	40	12	3667	2155	17	3	7	310
CHE01	2014	6	52	37	46	16	541	688	17	3	7	310
CHE03	2005	0	12	12	71	24	1171	1071	5	3	8	320
CLY01	2005	13	40	50	49	13	4475	2513	7	5	6	353
CLY01	2008	2	25	18	72	2	2738	2361	7	5	7	353
CLY01	2010	2	64	31	13	18	1806	1318	7	5	5	353
CLY01	2011	2	96	90	6	1	6760	660	7	5	6	353
CLY01	2012	2	46	29	15	39	713	441	7	5	6	353
CLY01	2013	4	47	52	15	20	436	262	7	5	6	353
CLY01	2014	2	78	63	22	10	420	147	7	5	5	353

COR01	2005	2	20	14	79	8	1234	1123	10	4	7	321
COR01	2007	1	27	28	115	14	538	227	10	4	6	321
COR01	2008	1	23	23	77	9	222	208	10	4	7	321
COR01	2009	2	37	37	49	17	874	611	10	4	6	321
COR01	2010	2	28	27	74	4	1486	1314	10	4	7	321
COR01	2011	2	51	53	44	4	4886	2514	10	4	7	321
COR01	2012	0	35	22	57	21	442	373	10	4	7	321
COR01	2013	2	30	24	65	17	1869	1475	10	4	7	321
COR01	2014	2	12	14	76	12	643	585	10	4	7	321
DUN01	2006	3	29	28	55	15	3588	2975	7	3	8	340
DUN01	2007	2	20	16	77	4	569	509	7	3	8	340
DUN01	2008	0	28	18	71	4	1198	1025	7	3	6	340
DUN01	2009	1	54	37	48	10	1820	1165	7	3	8	340
DUN01	2010	8	43	33	56	7	1070	857	7	3	7	340
DUN01	2011	1	33	33	61	3	1675	1165	7	3	6	340
DUN01	2012	3	37	30	64	11	215	178	7	3	8	340
DUN01	2013	0	40	25	63	12	401	343	7	3	7	340
DUN01	2014	3	41	29	40	20	1070	817	7	3	6	340
EFF01	2005	2	72	68	20	12	509	148	8	3	8	275
EFF01	2007	6	29	21	48	22	101	87	8	3	8	275
EFF01	2008	0	21	13	74	6	815	740	8	3	7	275
EFF01	2009	2	16	10	79	6	339	300	8	3	7	275
EFF01	2010	2	37	13	54	15	598	529	8	3	8	275
EFF01	2011	3	58	46	39	7	1128	561	8	3	8	275
EFF01	2012	2	32	18	60	18	623	508	8	3	8	275
EFF01	2013	7	34	9	63	20	210	191	8	3	8	275
EFF01	2014	3	73	65	23	9	4363	1462	8	3	8	275
FC01	2006	1	51	16	59	16	2369	1900	9	2	7	445
GB01	2006	8	20	17	59	18	1515	1335	11	2	7	348
GRA01	2005	4	39	40	52	8	3789	2511	28	3	7	306
GRA02	2005	8	24	32	41	26	1610	1295	36	3	6	288
GRA03	2005	3	46	54	29	14	1586	976	15	3	8	310
GRA03	2009	3	37	26	43	25	618	506	15	3	9	310
GRA03	2012	3	37	23	53	26	356	262	15	3	9	310
JB01	2008	2	25	18	72	2	2738	145	9	2	9	306
NAR01	2005	10	25	31	50	18	4175	3300	50	3	8	288
NAR02	2005	11	52	31	41	32	610	382	15	3	8	339
NAR02	2007	7	23	33	59	14	465	390	15	3	8	339
NB01	2006	7	60	39	35	17	1886	1153	7	2	7	208

SAR01	2006	4	29	16	51	20	344	311	15	2	8	344
SB01	2006	8	65	35	49	30	1308	715	1	3	7	159
SB01	2007	3	63	29	54	27	464	282	1	3	5	159
SB01	2008	2	58	49	37	38	583	197	1	3	7	159
SB01	2009	3	58	59	22	21	1016	397	1	3	7	159
SB01	2010	2	64	37	40	26	1444	848	1	3	7	159
SB01	2011	3	82	62	28	12	4263	1463	1	3	8	159
SB01	2012	4	58	38	37	38	1642	821	1	3	7	159
SB01	2013	1	73	26	53	36	1889	1067	1	3	8	159
SB01	2014	1	76	52	31	30	7500	2760	1	3	6	159
WB01	2005	10	67	8	40	16	2293	1371	6	4	7	208
WB01	2009	10	74	19	25	14	1783	683	6	4	6	208
WB01	2013	30	49	31	31	14	12400	8933	6	4	6	208

Table A6: Summary table showing difference in average air temperature for Cheticamp, North Mountain, and Ingonish weather stations monitored 2006-2016.

Response	Variable	Estimate	Standard Error	t-value
Average Air Temperature (˚C)	**Model 1 ~ Site + Factor (year)**			
	Intercept	17.98	0.21	84.00
	Cheticamp	0.40	0.15	2.25
	North Mountain	-2.18	0.16	-13.47
	Factor (Year) 2007	-0.48	0.40	-1.17
	Factor (Year) 2008	0.32	0.28	1.16
	Factor (Year) 2009	-0.78	0.28	-2.84
	Factor (Year) 2010	-0.33	0.28	-1.18
	Factor (Year) 2011	-1.27	0.28	-5.00
	Factor (Year) 2012	0.81	0.28	2.92
	Factor (Year) 2013	0.03	0.28	0.11
	Factor (Year) 2014	0.16	0.28	0.60
	Factor (Year) 2015	-0.77	0.31	-2.50
	Factor (Year) 2016	-0.41	0.28	-1.50
	Model 2 ~ Site			
	Intercept	18.50	0.21	86.61
	Ingonish	-0.36	0.29	-1.25
	North Mountain	-2.40	0.30	-7.90

Table A7: Summary table of average daily maximum, average, and maximum stream temperature for 12 streams monitored during summer 2006-2016. Models are arranged from lowest to highest ΔAIC_c value; only models with a $\Delta AIC_c < 8$ are shown.

Response	Variable	Estimate	Standard Error	t-value
Average Daily Maximum Stream Temperature (˚C)	**Model 6 ~ Grassland+ Factor (year) + Factor (order) + ADM air temperature**			
	Intercept	16.48	3.58	4.60
	Grassland	-0.15	0.03	-4.57
	Factor (year) 2007	1.60	0.79	2.04
	Factor (year) 2008	1.23	0.74	1.65
	Factor (year) 2009	0.75	0.66	1.14
	Factor (year) 2010	1.18	0.74	1.60
	Factor (year) 2011	0.14	0.75	0.19
	Factor (year) 2012	2.07	0.68	3.04
	Factor (year) 2013	1.71	0.75	2.30
	Factor (year) 2014	2.00	0.63	3.15
	Factor (year) 2015	1.09	0.74	1.47
	Factor (year) 2016	1.41	0.73	1.92
	Factor (order) 4	-0.31	0.51	-0.60
	Factor (order) 5	1.11	0.44	2.51
	ADM Air Temperature	0.01	0.16	0.07
	Model 7 ~ Grassland + Factor (year) + Factor (order) + Slope + ADM Air Temperature			
	Intercept	18.42	3.71	4.97
	Grassland	-0.16	0.03	-4.82
	Factor (year) 2007	1.62	0.77	2.10
	Factor (year) 2008	1.34	0.73	1.82
	Factor (year) 2009	0.78	0.65	1.20
	Factor (year) 2010	1.27	0.73	1.75
	Factor (year) 2011	0.09	0.73	0.12
	Factor (year) 2012	2.31	0.68	3.38
	Factor (year) 2013	1.91	0.74	2.57
	Factor (year) 2014	2.17	0.63	3.44
	Factor (year) 2015	1.06	0.73	1.45
	Factor (year) 2016	1.45	0.72	2.01
	Factor (order) 4	-0.45	0.51	-0.88
	Factor (order) 5	1.30	0.45	2.89
	ADM Air Temperature	-0.10	0.17	-0.61
	Slope	8.16	4.91	1.66

	Model 3 ~ Grassland + Factor (year) + ADM Air Temperature			
	Intercept	15.23	3.71	4.10
	Grassland	-0.17	0.03	-4.95
	Factor (year) 2007	1.71	0.82	2.09
	Factor (year) 2008	1.11	0.76	1.46
	Factor (year) 2009	0.77	0.69	1.11
	Factor (year) 2010	1.24	0.76	1.62
	Factor (year) 2011	0.29	0.77	0.38
	Factor (year) 2012	2.00	0.71	2.81
	Factor (year) 2013	1.55	0.76	2.02
	Factor (year) 2014	1.90	0.66	2.87
	Factor (year) 2015	1.12	0.77	1.45
	Factor (year) 2016	1.40	0.77	1.82
	ADM Air Temperature	0.08	0.16	0.48
	Model 8 ~ Grassland			
	Intercept	18.33	0.32	58.03
	Grassland	-0.19	0.03	-5.89
	Model 5 ~ Grassland + Factor (year) + ADM Air Temperature + Slope			
	Intercept	15.93	3.91	4.07
	Grassland	-0.17	0.03	-4.92
	Factor (year) 2007	1.73	0.82	2.10
	Factor (year) 2008	1.15	0.77	1.49
	Factor (year) 2009	0.77	0.70	1.12
	Factor (year) 2010	1.28	0.77	1.66
	Factor (year) 2011	0.28	0.77	0.34
	Factor (year) 2012	2.07	0.72	2.85
	Factor (year) 2013	1.61	0.78	2.08
	Factor (year) 2014	1.96	0.67	2.91
	Factor (year) 2015	1.11	0.78	1.42
	Factor (year) 2016	1.41	0.78	1.82
	ADM Air Temperature	0.04	0.17	0.21
	Slope	3.12	5.14	0.61
	Model 2 ~ Grassland + Factor (year) + Factor (order)			
	Intercept	16.85	0.61	27.48
	Grassland	-0.17	0.03	-5.22
	Factor (year) 2007	-0.24	0.50	-0.47
	Factor (year) 2008	1.17	0.44	2.68
	Factor (year) 2009	1.01	0.70	1.43
	Factor (year) 2010	1.20	0.74	1.62
	Factor (year) 2011	0.71	0.65	1.09
	Factor (year) 2012	1.15	0.74	1.56

	Factor (year) 2013	0.09	0.70	0.13
	Factor (year) 2014	2.04	0.67	3.05
	Factor (year) 2015	1.70	0.74	2.29
	Factor (year) 2016	1.97	0.63	3.14
	Factor (order) 4	1.01	0.73	1.38
	Factor (order) 5	1.44	0.70	2.06
	Null Model			
	Intercept	16.73	0.20	85.6
Average Stream Temperature (˚C)	**Model 3 ~ Grassland + Slope**			
	Intercept	15.52	0.37	42.62
	Grassland	-0.09	0.03	-3.76
	Slope	7.42	4.22	1.76
	Model 1 ~ Grassland			
	Intercept	15.93	0.28	56.34
	Grassland	-0.09	0.03	-3.09
	Model 4 ~ Grassland + Slope + Factor (order)			
	Intercept	15.40	0.39	39.66
	Grassland	-0.10	0.03	-3.25
	Slope	7.90	4.33	1.82
	Factor (order) 4	0.23	0.47	0.49
	Factor (order) 5	0.54	0.42	1.27
	Model 2 ~ Grassland + Factor (order)			
	Intercept	15.87	0.30	53.54
	Grassland	-0.10	0.03	-3.05
	Factor (order) 4	0.36	0.47	0.77
	Factor (order) 5	0.43	0.43	1.01
	Null Model			
	Intercept	15.17	0.15	100.2
Maximum Stream Temperature (˚C)	**Model 7 ~ Grassland + Maximum Air Temperature**			
	Intercept	18.86	4.70	4.01
	Grassland	-0.16	0.05	-2.76
	Maximum Air Temperature	0.14	0.14	1.01
	Model 8 ~ Grassland + Maximum Air Temperature + Factor (order)			
	Intercept	17.50	4.98	3.60
	Grassland	-0.17	0.05	-2.87
	Maximum Air Temperature	0.19	0.15	1.23
	Factor (order) 4	0.76	0.85	0.89
	Factor (order) 5	-0.08	0.74	-0.11
	Null Model			
	Intercept	22.05	0.27	81.48

Table A8: Summary table for total nitrogen and conductivity models for 21 streams monitored during summer 2005-2014. Models are arranged from lowest to highest ΔAIC_c value; only models with a $\Delta AIC_c < 8$ are shown, except for model containing only grassland; null models included.

Response	Variable	Estimate	Standard Error	t-value
Total Nitrogen (mg/L)	**Model 2 ~ Grassland + Factor (year) + Factor (order)**			
	Intercept	0.13	0.05	2.51
	Grassland	0.005	0.001	3.71
	Factor (year) 2006	0.09	0.04	2.21
	Factor (year) 2007	0.10	0.03	2.89
	Factor (year) 2008	0.03	0.03	0.96
	Factor (year) 2009	0.12	0.03	3.70
	Factor (year) 2010	0.11	0.03	3.15
	Factor (year) 2011	0.08	0.03	2.54
	Factor (year) 2012	0.08	0.03	2.37
	Factor (year) 2013	0.11	0.03	3.31
	Factor (year) 2014	0.06	0.03	1.65
	Factor (order) 3	-0.03	0.04	-0.67
	Factor (order) 4	0.008	0.05	0.18
	Factor (order) 5	-0.09	0.05	-1.89
	Model 1 ~ Grassland + Factor (year)			
	Intercept	0.09	0.03	2.92
	Grassland	0.005	0.001	3.97
	Factor (year) 2006	0.11	0.03	3.11
	Factor (year) 2007	0.11	0.03	3.15
	Factor (year) 2008	0.04	0.03	1.14
	Factor (year) 2009	0.13	0.03	3.92
	Factor (year) 2010	0.11	0.04	3.14
	Factor (year) 2011	0.09	0.03	2.57
	Factor (year) 2012	0.08	0.03	2.39
	Factor (year) 2013	0.12	0.03	3.31
	Factor (year) 2014	0.06	0.03	1.69
	Model 3 ~ Grassland + Factor (year) + Slope			
	Intercept	0.11	0.03	3.28
	Grassland	0.006	0.001	4.14
	Factor (year) 2006	0.10	0.03	2.97
	Factor (year) 2007	0.11	0.04	3.18
	Factor (year) 2008	0.04	0.03	1.15

	Factor (year) 2009	0.13	0.03	3.98
	Factor (year) 2010	0.11	0.04	3.17
	Factor (year) 2011	0.09	0.03	2.57
	Factor (year) 2012	0.09	0.04	2.54
	Factor (year) 2013	0.11	0.04	3.28
	Factor (year) 2014	0.06	0.03	1.75
	Slope	-0.20	0.14	-1.49
	Model 4 ~ Grassland + Factor (year) + Slope + Factor (order)			
	Intercept	0.13	0.05	2.59
	Grassland	0.006	0.002	3.46
	Factor (year) 2006	0.09	0.04	2.23
	Factor (year) 2007	0.10	0.03	2.92
	Factor (year) 2008	0.03	0.04	0.96
	Factor (year) 2009	0.13	0.03	3.75
	Factor (year) 2010	0.11	0.04	3.14
	Factor (year) 2011	0.08	0.03	2.52
	Factor (year) 2012	0.08	0.03	2.44
	Factor (year) 2013	0.11	0.03	3.26
	Factor (year) 2014	0.06	0.03	1.67
	Slope	-0.13	0.14	-0.93
	Factor (order) 3	-0.02	0.04	-0.53
	Factor (order) 4	0.02	0.05	0.38
	Factor (order) 5	-0.07	0.05	-1.47
	Model 5 ~ Grassland			
	Intercept	0.20	0.01	14.07
	Grassland	0.003	0.001	2.32
	Null Model			
	Intercept	0.22	0.008	25.35
Conductivity (µS/cm)	**Model 8 ~ Grassland + Elevation + Order**			
	Intercept	97.24	12.15	8.00
	Grassland	2.44	0.27	9.00
	Factor (order) 3	-36.16	7.79	-4.64
	Factor (order) 4	-30.65	9.25	-3.31
	Factor (order) 5	-23.07	9.78	-2.36
	Elevation	-0.11	0.03	-3.64
	Model 3 ~ Grassland			
	Intercept	33.85	3.43	9.86
	Grassland	2.22	0.30	7.38
	Null Model			
	Intercept	53.89	2.69	19.98

Table A9: Summary table for total and EPT macroinvertebrate abundance and functional feeding group models for 21 streams monitored during summer 2005-2014. Models are arranged from lowest to highest ΔAIC_c value. Only models that rank above the intercept and have a $\Delta AIC_c < 8$ are shown; null models included.

Response	Variable	Estimate	Standard Error	z-value
Total abundance (# of individuals)	**Model 5 ~ Grassland + Factor (year) + Factor (order) + Factor (substrate)**			
	Intercept	7.94	0.56	14.24
	Grassland	0.01	0.01	0.78
	Factor (year) 2006	-0.08	0.40	-0.02
	Factor (year) 2007	-0.98	0.37	-2.63
	Factor (year) 2008	-0.51	0.37	-1.39
	Factor (year) 2009	-0.38	0.35	-1.10
	Factor (year) 2010	-0.23	0.37	-0.61
	Factor (year) 2011	0.73	0.35	2.10
	Factor (year) 2012	-0.77	0.36	-2.12
	Factor (year) 2013	0.24	0.36	0.67
	Factor (year) 2014	0.04	0.35	0.13
	Factor (order) 3	-0.19	0.37	-0.50
	Factor (order) 4	-0.97	0.45	-2.14
	Factor (order) 5	-0.33	0.46	-0.72
	Factor (substrate) 6	0.16	0.30	0.53
	Factor (substrate) 7	0.07	0.31	0.22
	Factor (substrate) 8	-0.79	0.31	-2.54
	Factor (substrate) 9	-0.36	0.51	-0.70
	Model 3 ~ Grassland + Factor (year)+ Factor (substrate)			
	Intercept	7.79	0.42	18.58
	Grassland	0.008	0.01	0.62
	Factor (year) 2006	0.08	0.36	0.22
	Factor (year) 2007	-0.98	0.38	-2.58
	Factor (year) 2008	-0.44	0.38	-1.17
	Factor (year) 2009	-0.38	0.37	-1.06
	Factor (year) 2010	-0.35	0.37	-0.92
	Factor (year) 2011	0.62	0.38	1.73
	Factor (year) 2012	-0.79	0.37	-2.13
	Factor (year) 2013	0.19	0.37	0.52
	Factor (year) 2014	0.10	0.37	0.28
	Factor (substrate) 6	0.11	0.31	0.34

	Factor (substrate) 7	-0.12	0.30	-0.40
	Factor (substrate) 8	-0.81	0.32	-2.57
	Factor (substrate) 9	-0.29	0.52	-0.57
	Model 2 ~ Grassland + Factor (year) + Factor (order)			
	Intercept	7.91	0.53	15.07
	Grassland	0.003	0.01	0.22
	Factor (year) 2006	-0.06	0.42	-0.14
	Factor (year) 2007	-0.75	0.39	-1.93
	Factor (year) 2008	-0.48	0.38	-1.26
	Factor (year) 2009	-0.32	0.37	-0.87
	Factor (year) 2010	0.24	0.39	-0.62
	Factor (year) 2011	0.88	0.37	2.38
	Factor (year) 2012	-0.59	0.37	-1.59
	Factor (year) 2013	0.56	0.38	1.49
	Factor (year) 2014	0.27	0.37	0.73
	Factor (order) 3	-0.37	0.39	-0.95
	Factor (order) 4	-0.91	0.46	-1.98
	Factor (order) 5	-0.21	0.49	-0.43
	Null Model			
	Intercept	7.62	0.09	78.63
EPT abundance (# of EPT individuals)	**Model 5 ~ Grassland + Factor (year) + Factor (order) + Factor (substrate)**			
	Intercept	6.86	0.52	13.28
	Grassland	0.02	0.01	2.01
	Factor (year) 2006	0.05	0.37	0.14
	Factor (year) 2007	-0.81	0.35	-2.34
	Factor (year) 2008	-0.60	0.34	-1.65
	Factor (year) 2009	-0.18	0.32	-0.55
	Factor (year) 2010	0.002	0.034	0.007
	Factor (year) 2011	0.28	0.32	0.88
	Factor (year) 2012	-0.51	0.33	-1.52
	Factor (year) 2013	0.50	0.34	1.48
	Factor (year) 2014	-0.07	0.33	-0.22
	Factor (order) 3	0.23	0.34	0.67
	Factor (order) 4	-0.48	0.42	-1.16
	Factor (order) 5	-0.08	0.43	-0.18
	Factor (substrate) 6	0.06	0.28	0.20
	Factor (substrate) 7	0.21	0.29	0.72
	Factor (substrate) 8	-0.79	0.28	-2.74
	Factor (substrate) 9	-1.30	0.48	-2.73
	Model 3 ~ Grassland + Factor (year) + Factor (substrate)			
	Intercept	7.12	0.39	18.31
	Grassland	0.02	0.01	1.80

	Factor (year) 2006	0.11	0.33	0.33
	Factor (year) 2007	-0.75	0.35	-2.13
	Factor (year) 2008	-0.49	0.35	-1.42
	Factor (year) 2009	-0.21	0.33	-0.64
	Factor (year) 2010	-0.09	0.35	-0.26
	Factor (year) 2011	0.22	0.33	0.67
	Factor (year) 2012	-0.51	0.34	-1.48
	Factor (year) 2013	0.51	0.35	1.48
	Factor (year) 2014	-0.02	0.33	-0.06
	Factor (substrate) 6	-0.03	0.29	-0.11
	Factor (substrate) 7	0.01	0.28	0.03
	Factor (substrate) 8	-0.78	0.29	-2.69
	Factor (substrate) 9	-1.34	0.48	-2.80
	Null model			
	Intercept	7.08	0.09	78.35
Shredders (%)	**Model 2 ~ Grassland + Factor (year) + Factor (order)**			
	Intercept	2.80	0.37	7.56
	Grassland	-0.01	0.01	-1.10
	Factor (year) 2006	-0.02	0.29	-0.06
	Factor (year) 2007	-0.08	0.27	-0.31
	Factor (year) 2008	-0.11	0.27	-0.39
	Factor (year) 2009	0.09	0.27	0.36
	Factor (year) 2010	-0.21	0.28	-0.76
	Factor (year) 2011	-0.86	0.28	-3.10
	Factor (year) 2012	0.34	0.26	1.31
	Factor (year) 2013	0.17	0.26	0.63
	Factor (year) 2014	0.06	0.26	0.02
	Factor (order) 3	0.30	0.27	1.09
	Factor (order) 4	-0.26	0.33	-0.79
	Factor (order) 5	-0.08	0.35	-0.24
	Model 5 ~ Grassland + Factor (year) + Factor(order) + Factor (substrate)			
	Intercept	3.29	0.41	8.04
	Grassland	-0.08	0.10	-0.85
	Factor (year) 2006	-0.07	0.29	-0.25
	Factor (year) 2007	-0.06	0.27	-0.22
	Factor (year) 2008	-0.11	0.27	-0.40
	Factor (year) 2009	0.017	0.26	0.07
	Factor (year) 2010	-0.33	0.28	-1.19
	Factor (year) 2011	-0.97	0.27	-3.52
	Factor (year) 2012	0.34	0.26	1.31
	Factor (year) 2013	0.11	0.27	0.41
	Factor (year) 2014	-0.10	0.26	-0.38

	Factor (order) 3	0.25	0.27	0.90
	Factor (order) 4	-0.30	0.34	-0.89
	Factor (order) 5	-0.20	0.35	-0.59
	Factor (substrate) 6	-0.48	0.22	-2.19
	Factor (substrate) 7	-0.41	0.22	-1.85
	Factor (substrate) 8	-0.52	0.22	-2.33
	Factor (substrate) 9	-0.66	0.37	-1.78
	Null Model			
	Intercept	2.88	0.06	42.43
Grazers (%)	**Model 5 ~ Grassland + Factor (year) + Factor (order) + Factor (substrate)**			
	Intercept	3.35	0.27	12.35
	Grassland	0.01	0.01	0.86
	Factor (year) 2006	0.08	0.19	0.44
	Factor (year) 2007	0.25	0.18	1.41
	Factor (year) 2008	0.28	0.17	1.63
	Factor (year) 2009	-0.16	0.17	-0.96
	Factor (year) 2010	0.15	0.18	0.83
	Factor (year) 2011	-0.36	0.17	-2.10
	Factor (year) 2012	-0.002	0.18	-0.02
	Factor (year) 2013	0.12	0.18	0.67
	Factor (year) 2014	-0.06	0.17	-0.33
	Factor (order) 3	0.02	0.18	0.11
	Factor (order) 4	0.40	0.22	1.87
	Factor (order) 5	-0.36	0.23	-1.58
	Factor (substrate) 6	0.21	0.15	1.34
	Factor (substrate) 7	0.39	0.16	2.50
	Factor (substrate) 8	0.46	0.16	2.95
	Factor (substrate) 9	0.53	0.25	2.15
	Model 2 ~ Grassland + Factor (year) + Factor (order)			
	Intercept	3.73	0.25	15.09
	Grassland	0.01	0.01	0.96
	Factor (year) 2006	0.09	0.20	0.46
	Factor (year) 2007	0.15	0.18	0.83
	Factor (year) 2008	0.34	0.18	1.89
	Factor (year) 2009	-0.19	0.18	-1.08
	Factor (year) 2010	0.06	0.19	0.31
	Factor (year) 2011	-0.39	0.18	-2.19
	Factor (year) 2012	-0.05	0.18	-0.29
	Factor (year) 2013	0.01	0.18	-0.05
	Factor (year) 2014	-0.18	0.18	-1.02
	Factor (order) 3	0.02	0.18	0.12
	Factor (order) 4	0.42	0.21	1.94

	Factor (order) 5	-0.522	0.23	-2.21
	Null Model			
	Intercept	3.82	0.05	78.05
Predators (%)	**Model 7 ~ Grassland + Factor (year) + Factor (order) + Elevation**			
	Intercept	3.95	0.34	11.65
	Grassland	-0.003	0.01	-0.42
	Factor (year) 2006	-0.017	0.22	-0.74
	Factor (year) 2007	-0.23	0.21	-1.09
	Factor (year) 2008	-0.42	0.21	-2.00
	Factor (year) 2009	-0.006	0.20	-0.03
	Factor (year) 2010	-0.29	0.21	-1.35
	Factor (year) 2011	0.52	0.20	2.66
	Factor (year) 2012	-0.19	0.20	-0.95
	Factor (year) 2013	-0.24	0.20	-1.20
	Factor (year) 2014	0.10	0.20	0.51
	Factor (order) 3	0.05	0.21	0.22
	Factor (order) 4	-0.14	0.25	-0.58
	Factor (order) 5	0.44	0.26	1.67
	Elevation	-0.001	0.0007	-1.93
	Model 2 ~ Grassland + Factor (year) + Factor (order)			
	Intercept	3.62	0.29	12.55
	Grassland	-0.01	0.01	-1.04
	Factor (year) 2006	-0.21	0.23	-0.95
	Factor (year) 2007	-0.29	0.21	-1.36
	Factor (year) 2008	-0.46	0.20	-2.17
	Factor (year) 2009	-0.03	0.20	-0.15
	Factor (year) 2010	-0.34	0.22	-1.57
	Factor (year) 2011	0.47	0.20	2.37
	Factor (year) 2012	-0.24	0.20	-1.20
	Factor (year) 2013	-0.29	0.21	-1.39
	Factor (year) 2014	0.06	0.20	0.30
	Factor (order) 3	0.04	0.21	0.21
	Factor (order) 4	-0.18	0.25	-0.71
	Factor (order) 5	0.34	0.27	1.28
	Model 4 ~ Grassland + Factor (year) + Elevation			
	Intercept	3.97	0.26	15.23
	Grassland	-0.01	0.01	-0.10
	Factor (year) 2006	-0.27	0.21	-1.29
	Factor (year) 2007	-0.34	0.22	-1.54
	Factor (year) 2008	-0.50	0.22	-2.31
	Factor (year) 2009	-0.12	0.20	-0.57
	Factor (year) 2010	-0.35	0.22	-1.58

	Factor (year) 2011	0.47	0.20	2.30
	Factor (year) 2012	-0.25	0.21	-1.21
	Factor (year) 2013	-0.28	0.21	-1.32
	Factor (year) 2014	0.07	0.21	0.34
	Elevation	-0.001	0.001	-1.29
	Model 8 ~ Grassland + Factor (year) + Factor (substrate) + Elevation			
	Intercept	4.40	0.36	12.08
	Grassland	-0.005	0.008	-0.60
	Factor (year) 2006	-0.17	0.20	-0.82
	Factor (year) 2007	-0.37	0.22	-1.69
	Factor (year) 2008	-0.37	0.22	-1.69
	Factor (year) 2009	-0.11	0.20	-0.53
	Factor (year) 2010	-0.40	0.22	-1.79
	Factor (year) 2011	0.46	0.20	2.32
	Factor (year) 2012	-0.28	0.21	-1.33
	Factor (year) 2013	-0.36	0.21	-1.70
	Factor (year) 2014	0.03	0.20	0.17
	Factor (substrate) 6	-0.07	0.19	-0.38
	Factor (substrate) 7	-0.36	0.19	-1.85
	Factor (substrate) 8	-0.27	0.19	-1.40
	Factor (substrate) 9	-0.46	0.31	-1.50
	Elevation	-0.002	0.0008	-2.15
	Model 6 ~ Grassland + Factor (year) + Factor (substrate) + Factor (order) + Elevation			
	Intercept	4.24	0.43	9.92
	Grassland	-0.001	0.008	-0.18
	Factor (year) 2006	-0.10	0.23	-0.45
	Factor (year) 2007	-0.26	0.22	-1.23
	Factor (year) 2008	-0.33	0.21	-1.56
	Factor (year) 2009	-0.01	0.20	-0.05
	Factor (year) 2010	-0.32	0.21	-1.53
	Factor (year) 2011	0.50	0.19	2.62
	Factor (year) 2012	-0.21	0.21	-1.02
	Factor (year) 2013	-0.30	0.21	-1.45
	Factor (year) 2014	0.07	0.20	0.36
	Factor (substrate) 6	-0.07	0.18	-0.37
	Factor (substrate) 7	-0.26	0.20	-1.30
	Factor (substrate) 8	-0.19	0.19	-1.01
	Factor (substrate) 9	-0.39	0.31	-1.28
	Factor (order) 3	0.06	0.21	0.27
	Factor (order) 4	-0.07	0.26	-0.27
	Factor (order) 5	0.38	0.26	1.46

	Elevation	-0.002	0.001	-2.33
	Model 3 ~ Grassland + Factor (year) + Factor (substrate)			
	Intercept	3.80	0.24	15.78
	Grassland	-0.01	0.008	-1.32
	Factor (year) 2006	-0.23	0.21	-1.09
	Factor (year) 2007	-0.41	0.22	-1.87
	Factor (year) 2008	-0.43	0.22	-1.96
	Factor (year) 2009	-0.10	0.20	-0.50
	Factor (year) 2010	-0.40	0.22	-1.82
	Factor (year) 2011	0.42	0.20	2.07
	Factor (year) 2012	-0.31	0.22	-1.42
	Factor (year) 2013	-0.38	0.22	-1.75
	Factor (year) 2014	0.03	0.21	0.15
	Factor (substrate) 6	0.06	0.18	0.34
	Factor (substrate) 7	-0.16	0.18	-0.93
	Factor (substrate) 8	-0.09	0.18	-0.47
	Factor (substrate) 9	-0.29	0.31	-0.95
	Model 5 ~ Grassland + Factor (year) + Factor (substrate) + Factor (order)			
	Intercept	3.61	0.33	11.00
	Grassland	-0.01	0.01	-0.98
	Factor (year) 2006	-0.19	0.23	-0.80
	Factor (year) 2007	-0.32	0.22	-1.48
	Factor (year) 2008	-0.40	0.22	-1.84
	Factor (year) 2009	-0.01	0.20	-0.07
	Factor (year) 2010	-0.33	0.22	-1.53
	Factor (year) 2011	0.47	0.20	2.35
	Factor (year) 2012	-0.24	0.21	-1.12
	Factor (year) 2013	-0.32	0.21	-1.49
	Factor (year) 2014	0.07	0.20	0.32
	Factor (substrate) 6	0.09	0.18	0.51
	Factor (substrate) 7	-0.04	0.18	-0.23
	Factor (substrate) 8	-0.01	0.18	-0.05
	Factor (substrate) 9	-0.23	0.31	-0.75
	Factor (order) 3	0.05	0.22	0.23
	Factor (order) 4	-0.16	0.27	-0.61
	Factor (order) 5	0.29	0.27	1.09
	Null Model			
	Intercept	3.50	0.05	63.39
Filterers (%)	**Model 6 ~ Grassland + Factor (order) + Factor (substrate) + Elevation**			
	Intercept	2.05	0.71	2.86
	Grassland	0.03	0.01	2.63

	Factor (order) 3	-0.02	0.33	-0.05
	Factor (order) 4	-1.07	0.46	-2.34
	Factor (order) 5	-0.23	0.44	-0.52
	Factor (substrate) 6	0.39	0.34	1.14
	Factor (substrate) 7	-0.15	0.36	-0.43
	Factor (substrate) 8	-0.33	0.36	-0.92
	Factor (substrate) 9	-0.63	0.58	-1.09
	Elevation	-0.003	0.001	-1.76
	Model 5 ~ Grassland + Factor (order) + Factor (substrate)			
	Intercept	1.04	0.45	2.33
	Grassland	0.02	0.01	2.09
	Factor (order) 3	0.07	0.33	0.20
	Factor (order) 4	-1.11	0.46	-2.41
	Factor (order) 5	-0.30	0.45	-0.66
	Factor (substrate) 6	0.63	0.33	1.93
	Factor (substrate) 7	0.13	0.33	0.39
	Factor (substrate) 8	-0.11	0.34	-0.32
	Factor (substrate) 9	-0.41	0.58	-0.72
	Model 8 ~ Grassland + Factor (substrate) + Elevation			
	Intercept	2.37	0.63	3.79
	Grassland	0.03	0.01	2.58
	Factor (substrate) 6	0.27	0.36	0.75
	Factor (substrate) 7	-0.39	0.36	-1.10
	Factor (substrate) 8	-0.38	0.38	-1.02
	Factor (substrate) 9	-0.67	0.59	-1.12
	Elevation	-0.004	0.002	-2.41
	Model 7 ~ Grassland + Factor (order) + Elevation			
	Intercept	1.92	0.54	3.51
	Grassland	0.02	0.01	2.12
	Factor (order) 3	0.13	0.34	0.38
	Factor (order) 4	-0.94	0.48	-1.96
	Factor (order) 5	0.21	0.46	0.45
	Elevation	-0.003	0.001	-1.86
	Model 2 ~ Grassland + Factor (order)			
	Intercept	1.15	0.36	3.22
	Grassland	0.02	0.01	1.62
	Factor (order) 3	0.18	0.35	0.52
	Factor (order) 4	-0.97	0.48	-2.01
	Factor (order) 5	0.07	0.46	0.15
	Model 1 ~ Grassland			
	Intercept	1.23	0.15	8.12
	Grassland	0.02	0.01	1.45
	Model 4 ~ Grassland + Elevation			

	Intercept	2.07	0.43	4.80
	Grassland	0.02	0.01	1.95
	Elevation	-0.003	0.001	-2.07
	Model 3 ~ Grassland + Factor (substrate)			
	Intercept	1.04	0.31	3.39
	Grassland	0.02	0.01	1.79
	Factor (substrate) 6	0.60	0.34	1.73
	Factor (substrate) 7	-0.01	0.34	-0.03
	Factor (substrate) 8	-0.03	0.36	-0.09
	Factor (substrate) 9	-0.35	0.60	-0.59
	Null Model			
	Intercept	1.41	0.10	14.74
Gatherers (%)	**Model 6 ~ Grassland + Factor (year) + Factor (substrate) + Factor (order) + Elevation**			
	Intercept	5.11	0.34	15.18
	Grassland	-0.02	0.006	-2.67
	Factor (year) 2006	-0.02	0.18	-0.10
	Factor (year) 2007	-0.29	0.17	-1.67
	Factor (year) 2008	-0.44	0.17	-2.59
	Factor (year) 2009	-0.14	0.16	-0.90
	Factor (year) 2010	-0.19	0.17	-1.15
	Factor (year) 2011	0.26	0.15	1.68
	Factor (year) 2012	-0.16	0.16	-0.99
	Factor (year) 2013	-0.19	0.16	-1.18
	Factor (year) 2014	-0.07	0.16	-0.44
	Factor (substrate) 6	-0.37	0.14	-2.56
	Factor (substrate) 7	-0.52	0.16	-3.39
	Factor (substrate) 8	-0.58	0.15	-3.90
	Factor (substrate) 9	-0.56	0.24	-2.30
	Factor (order) 3	0.02	0.17	0.12
	Factor (order) 4	-0.35	0.21	-1.66
	Factor (order) 5	0.08	0.21	0.38
	Elevation	-0.002	0.001	-3.07
	Model 8 ~ Grassland + Factor (year) + Factor (substrate) + Elevation			
	Intercept	5.32	0.29	18.18
	Grassland	-0.02	0.01	-2.83
	Factor (year) 2006	0.006	0.18	0.04
	Factor (year) 2007	-0.34	0.18	-1.93
	Factor (year) 2008	-0.45	0.16	-2.55
	Factor (year) 2009	-0.21	0.17	-1.27
	Factor (year) 2010	-0.26	0.17	-1.51
	Factor (year) 2011	0.22	0.16	1.36

	Factor (year) 2012	-0.23	0.17	-1.34
	Factor (year) 2013	-0.25	0.17	-1.47
	Factor (year) 2014	-0.10	0.17	-0.59
	Factor (substrate) 6	-0.42	0.15	-2.93
	Factor (substrate) 7	-0.67	0.15	-4.36
	Factor (substrate) 8	-0.64	0.16	-4.14
	Factor (substrate) 9	-0.59	0.25	-2.38
	Elevation	-0.002	0.001	-3.50
	Model 7 ~ Grassland + Factor (year) + Factor (order) + Elevation			
	Intercept	4.34	0.29	15.04
	Grassland	-0.02	0.01	-3.16
	Factor (year) 2006	-0.08	0.19	-0.43
	Factor (year) 2007	-0.25	0.18	-1.38
	Factor (year) 2008	-0.51	0.18	-2.82
	Factor (year) 2009	-0.07	0.17	-0.39
	Factor (year) 2010	-0.06	0.18	-0.32
	Factor (year) 2011	0.31	0.17	1.83
	Factor (year) 2012	-0.09	0.17	-0.55
	Factor (year) 2013	-0.09	0.17	-0.51
	Factor (year) 2014	0.06	0.17	0.34
	Factor (order) 3	0.01	0.18	0.08
	Factor (order) 4	-0.43	0.21	-2.03
	Factor (order) 5	0.16	0.22	0.71
	Elevation	-0.001	0.001	-1.40
	Model 2 ~ Grassland + Factor (year) + Factor (order)			
	Intercept	4.13	0.24	16.86
	Grassland	-0.03	0.01	-3.73
	Factor (year) 2006	-0.11	0.19	-0.60
	Factor (year) 2007	-0.29	0.18	-1.61
	Factor (year) 2008	-0.54	0.18	-3.00
	Factor (year) 2009	-0.08	0.17	-0.50
	Factor (year) 2010	-0.10	0.18	-0.55
	Factor (year) 2011	0.27	0.17	1.61
	Factor (year) 2012	-0.14	0.17	-0.77
	Factor (year) 2013	-0.12	0.18	-0.67
	Factor (year) 2014	0.02	0.17	0.13
	Factor (order) 3	0.03	0.18	0.15
	Factor (order) 4	-0.44	0.22	-2.04
	Factor (order) 5	0.12	0.23	0.51
	Model 5 ~ Grassland + Factor (year) + Factor (order) + Factor (substrate)			
	Intercept	4.43	0.27	16.55

	Grassland	-0.02	0.01	-3.72
	Factor (year) 2006	-0.11	0.18	-0.58
	Factor (year) 2007	-0.36	0.18	-2.00
	Factor (year) 2008	-0.53	0.18	-2.97
	Factor (year) 2009	-0.15	0.17	-0.90
	Factor (year) 2010	-0.21	0.18	-1.16
	Factor (year) 2011	0.21	0.16	1.29
	Factor (year) 2012	-0.20	0.17	-1.17
	Factor (year) 2013	-0.22	0.17	-1.23
	Factor (year) 2014	-0.09	0.17	-0.53
	Factor (order) 3	0.05	0.18	0.27
	Factor (order) 4	-0.41	0.22	-1.86
	Factor (order) 5	0.02	0.22	0.09
	Factor (substrate) 6	-0.19	0.14	-1.37
	Factor (substrate) 7	-0.29	0.15	-2.03
	Factor (substrate) 8	-0.39	0.15	-2.67
	Factor (substrate) 9	-0.37	0.25	-1.48
	Null Model			
	Intercept	3.82	0.05	77.53

Functional Feeding Group Composition

In general, the results pertaining to functional feeding groups show evidence to support the River Continuum Concept (RCC). Shredding invertebrates were found to decrease in abundance from lower order to higher order streams, while grazing invertebrates increased in abundance from lower order to higher order streams. Predators were expected to stay relatively the same throughout the study streams; however, evidence suggests that they increase in abundance from lower order to higher order streams. Collector-gathering invertebrates were found to decrease from lower order to higher order streams, while filter-feeding invertebrates were found to be not related to stream order. These results are relatively consistent with the RCC that predicts changes in functional feeding group dominance in a downstream pattern as food availability changes (Vannote et al. 1980).

Another reason for patterns in functional feeding groups relates to year-to-year variation. For the 7 sites that were sampled annually, the percentages of functional feeding groups were outlined to demonstrate year-to-year variability (Figure A1). Collector-gatherers dominate the functional feeding groups for Branch Pond, Clyburn, and Still Brook, while grazing invertebrates dominate the sites Benjie's, Corny, Dundas, and Effie's. This suggests the former sites have higher FPOM inputs, while the latter have more algae present. However, yearly trends show that basal resources can shift due to decreases observed in specific functional feeding groups. For instance, Benjie's shows a shift from grazer dominance in 2008-2010, to more collector-gatherer dominated assemblages in 2011-2012. All feeding groups show general natural variation to year,

however, 2011, there is a general decrease in grazers with an increase in gatherers and predators. This shift in feeding group dominance is most likely due to an alteration in food resources or physio-chemical changes.

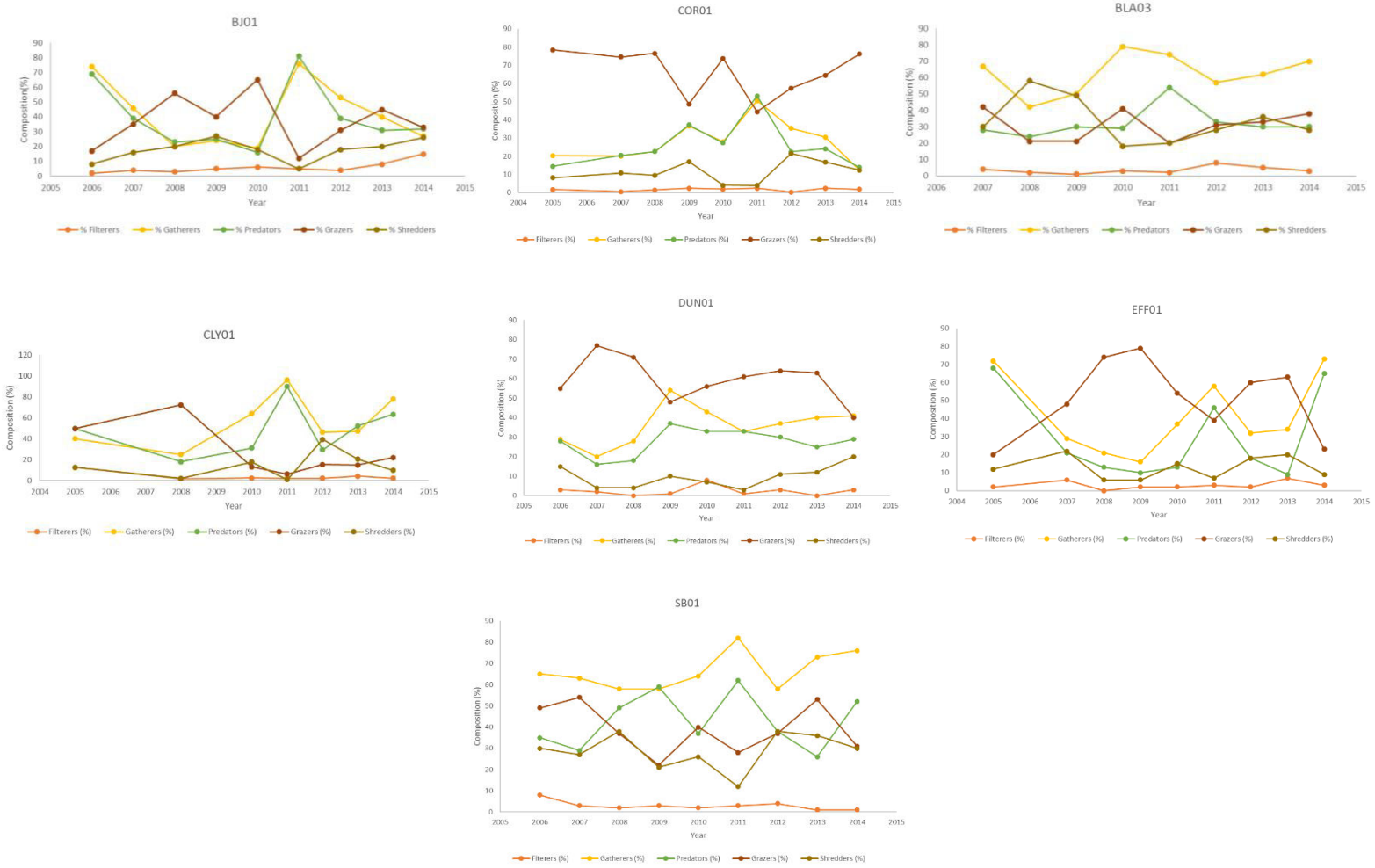

Figure A1. Functional feeding groups for 7 regularly monitored Parks Canada sites sampled during fall 2005- 2014.

APPENDIX B – Additional data and results for Chapter 3

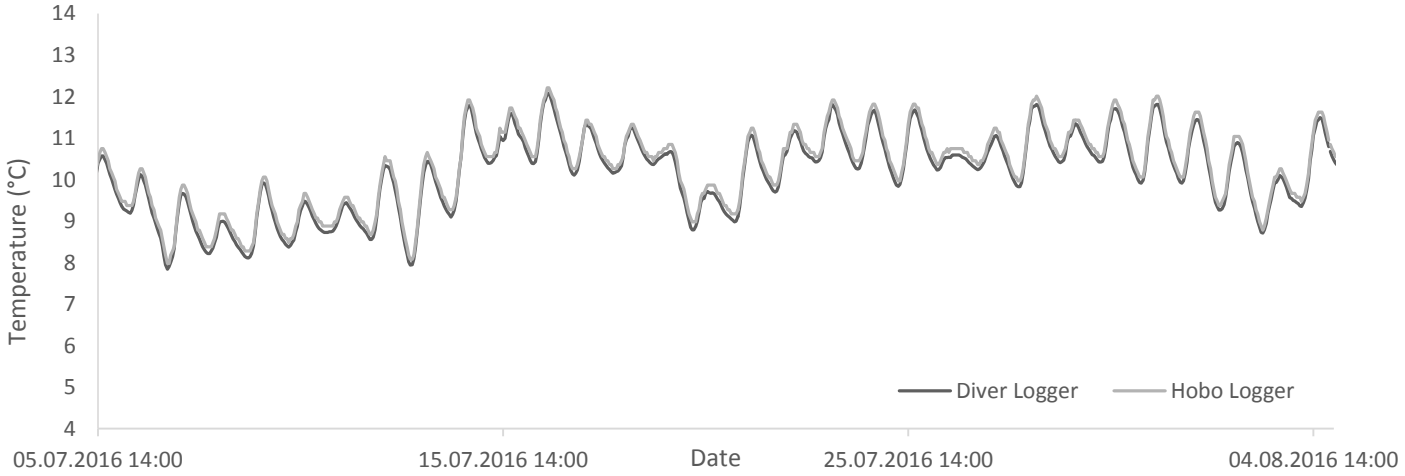

Figure B1: Margaree River stream (MAR02) comparison of diver and hobo stream temperature loggers July 5-August 5, 2016.

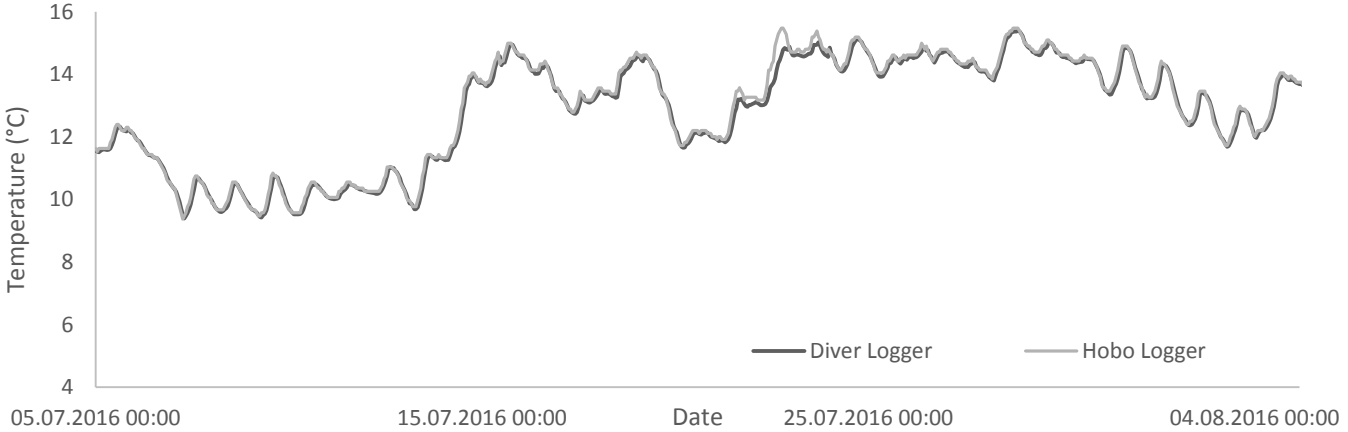

Figure B2: Phillips Cove stream (PC01) comparison of diver and hobo stream temperature loggers July 5-August 5, 2016.

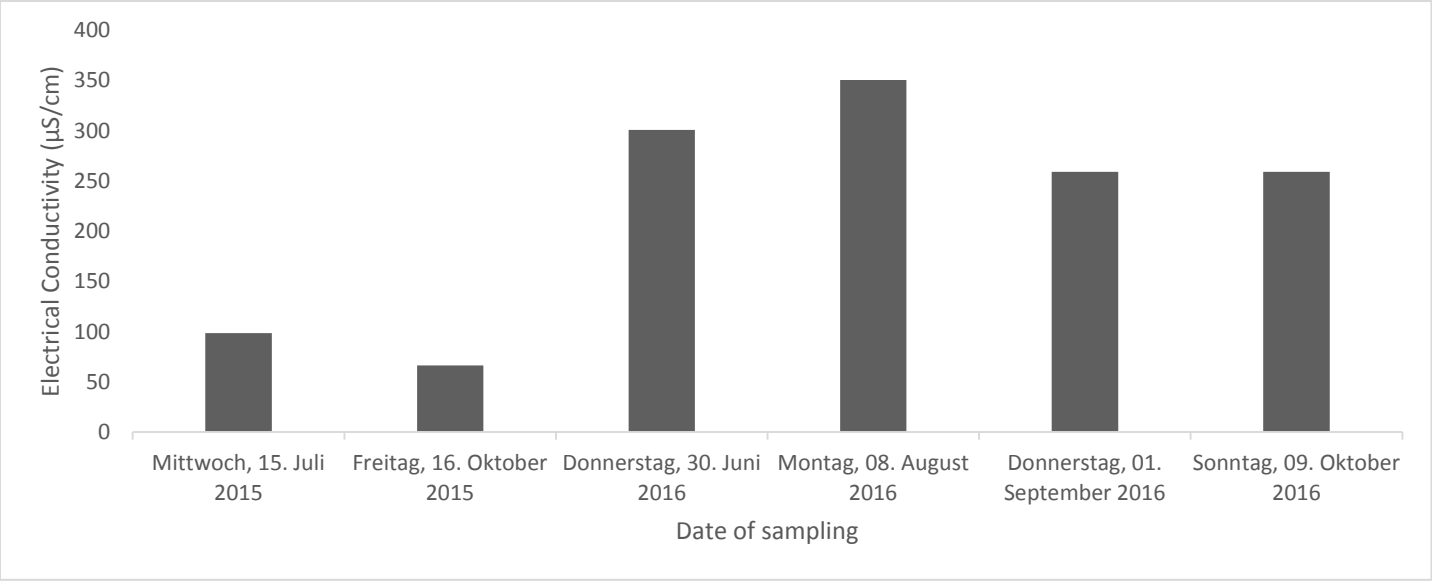

Figure B3: Electrical conductivity values for Benjie's Lake Brook before (2015) and after (2016) road construction.

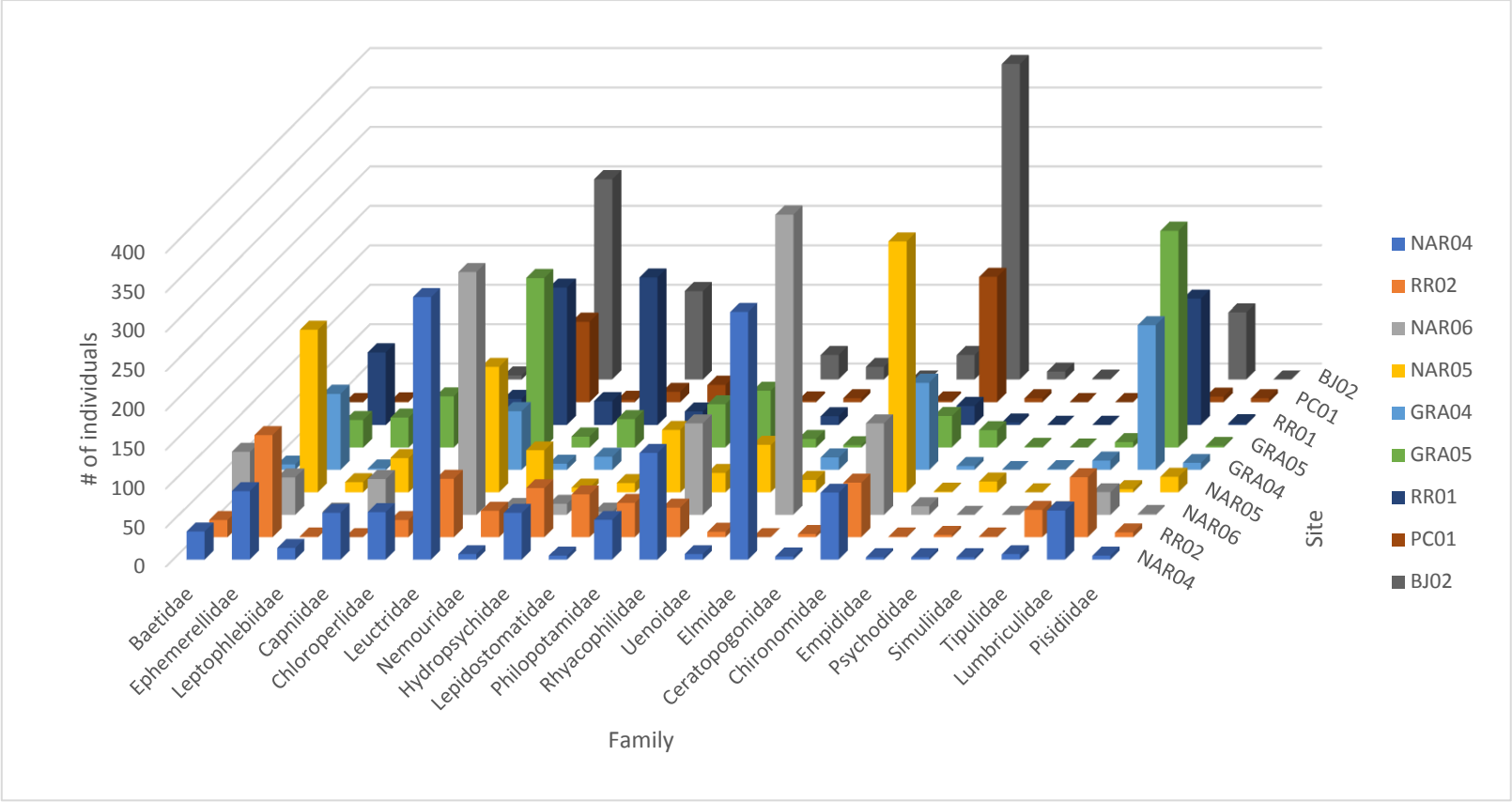

Figure B4: Total number of individuals per family level macroinvertebrate taxa for 9 headwater streams sampled October 2016. Sites are ordered (near to far) from highest to lowest grassland percentage. Grassland sites: North Aspy River streams (NAR04, NAR05, NAR06), Red River streams (RR01, RR02), Grande Anse River streams (GRA04, GRA05), Forested sites: Philip's Cove Brook (PC01) and Benjie's Lake Brook (BJ02).

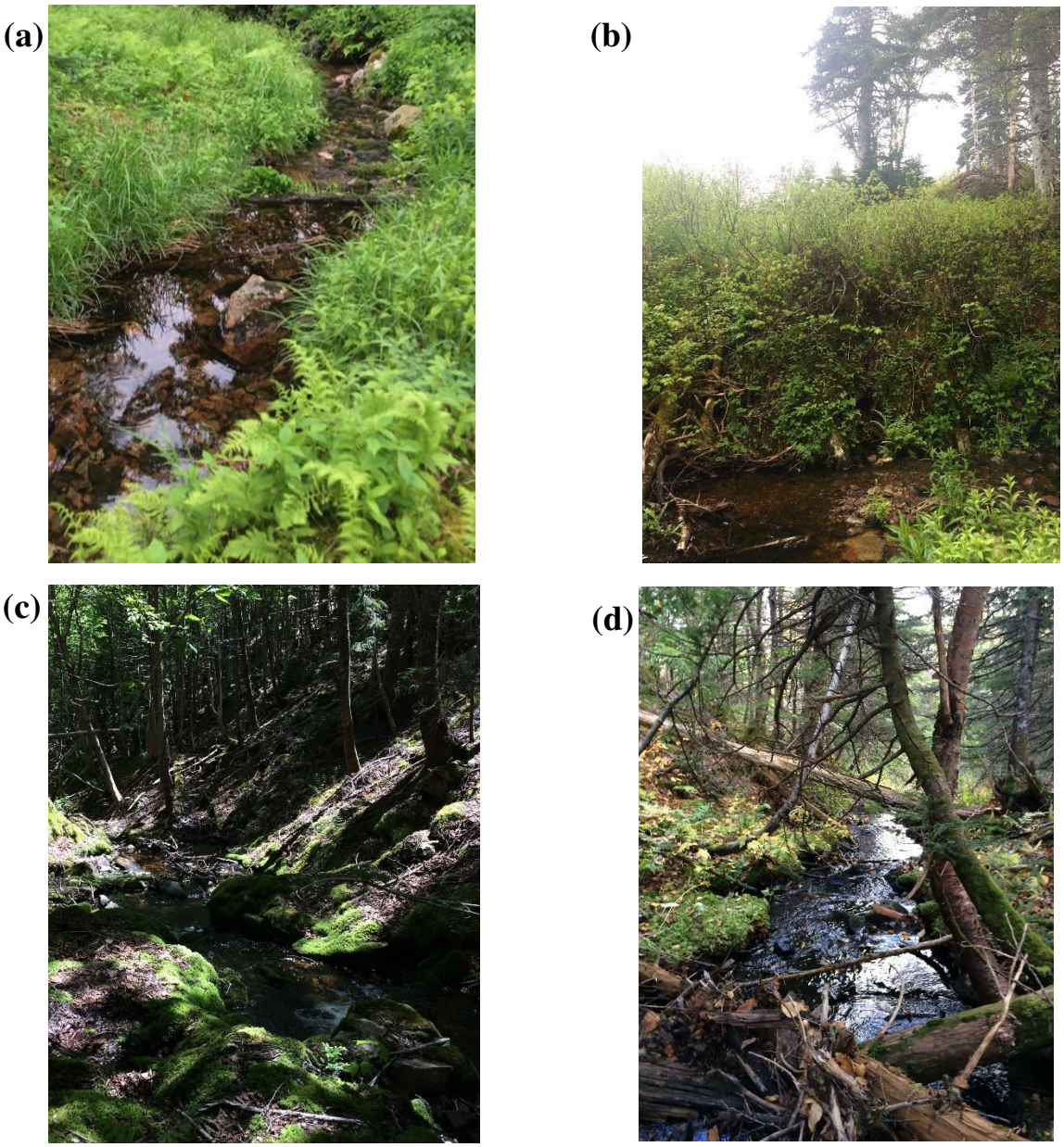

Figure B5: Examples of grassland dominated streams (top) and forest dominated streams. (a) Grande Anse River stream (GRA04), (b) North Aspy River stream (NAR04), (c) Benjie's Lake Brook (BJ02), and (d) Fishing Cove River stream (FC03).

Table B1: General site characteristics of streams in different regions of Cape Breton Highlands (GPS Datum: WGS 84).

Site Code	Basin Name	Northing	Easting	Stream Order	Substrate Diameter mean (cm)	Slope (m/m)	Elevation (m)	Size (km2)	Stream Discharge (m3/s)	Dominant Streamside Vegetation	Grassland (%)	Alders (%)	Wetlands (%)
BJ02	Benjie's Lake Brook	664606	5184717	2	10.60	0.20	280	0.32	3.61	White birch	0	6	0
FC02	Fishing Cove River	665368	5178117	1	13.37	0.09	405	0.38	4.19	Speckled alder	0	30	0
FC03	Fishing Cove River	665272	5178433	1	11.08	0.05	420	0.17	1.88	Balsam fir	4	60	0
FC04	Fishing Cove River	665957	5177363	1	13.47	0.06	420	0.80	4.19	Speckled alder	0	54	0
PC01	Phillip's Cove Brook	663394	5185564	2	12.46	0.04	225	0.39	3.28	Balsam fir	0	5	0
MAR01	Northeast Margaree River	668179	5162057	1	7.94	0.03	400	0.55	5.49	Balsam fir	0	11	0
MAR02	Northeast Margaree River	668491	5162125	1	5.44	0.07	405	0.42	1.73	Speckled alder	0	12	0
GRA04	Grande Anse River	675941	5185403	2	9.61	0.09	410	0.29	1.25	Grasses, fern sp.	49	0	27
GRA05	Grande Anse River	675862	5185289	2	5.50	0.11	410	0.41	10.32	Speckled alder	42	1	30
NAR04	North Aspy River	678429	5187596	1	10.48	0.06	420	0.46	2.19	Speckled alder	55	17	0
NAR05	North Aspy River	678475	5188302	1	9.08	0.05	415	0.51	2.10	Speckled alder	69	18	2
NAR06	North Aspy River	678983	5188403	1	9.85	0.04	420	0.45	6.59	Speckled alder	51	30	0
RR01	Red River	676515	5187148	1	10.66	0.14	415	0.18	1.47	Grasses, fern sp.	28	12	0
RR02	Red River	676385	5187356	1	15.63	0.04	415	0.32	2.27	Speckled alder	61	0	19

Table B2: Stream temperature (average daily maximum, average, maximum, minimum, and average daily temperature range) variables used in the analysis of moose impacts on 13 headwater streams.

Site	Average Daily Maximum	Average Temperature	Maximum	Minimum	Average Daily Range
BJ02	13.87	12.84	17.19	8.58	1.87
FC03	13.74	12.60	16.05	7.78	2.21
FC04	14.64	13.22	17.79	8.26	2.60
MAR01	13.45	11.85	16.81	7.28	3.18
MAR02	11.22	10.54	12.69	7.98	1.31
GRA04	15.51	13.16	20.04	6.98	3.84
GRA05	13.64	12.04	16.05	7.38	2.82
NAR04	16.02	13.36	20.71	7.98	4.69
NAR05	14.21	12.75	17.02	8.23	2.77
NAR06	15.05	13.52	18.62	8.78	2.80
RR01	13.98	12.33	16.55	8.81	2.75
RR02	12.98	11.77	15.09	7.98	2.48

Table B3: Total nitrogen and stream conductivity values used in moose impact analysis for 14 study streams sampled monthly June-October 2016.

Sample Date	Site	Total Nitrogen (mg/L)	Conductivity (µS/cm)
30-Jun	BJ02	0.14	302.46
08-Aug	BJ02	0.14	342.42
02-Sep	BJ02	0.2	253.60
07-Oct	BJ02	0.29	259.00
05-Aug	FC02	0.21	38.68
30-Jun	FC02	0.22	39.43
13-Oct	FC02	0.26	45.51
02-Sep	FC02	0.44	58.28
29-Jun	FC03	0.22	30.46
13-Oct	FC03	0.22	39.05
05-Aug	FC03	0.24	40.45
02-Sep	FC03	0.43	57.43
13-Oct	FC04	0.22	37.38
29-Jun	FC04	0.23	42.91
05-Aug	FC04	0.23	55.11
02-Sep	FC04	0.42	67.82
01-Sep	GRA04	0.61	44.78
04-Aug	GRA04	0.63	45.98
05-Oct	GRA04	0.66	50.55
29-Jun	GRA04	0.7	54.15
29-Jun	GRA05	0.45	88.43
04-Aug	GRA05	0.47	89.64
05-Oct	GRA05	0.57	94.94
01-Sep	GRA05	0.84	109.46
04-Jul	MAR01	0.12	33.72
09-Aug	MAR01	0.12	37.67
14-Oct	MAR01	0.14	38.37
05-Sep	MAR01	0.17	40.38
04-Jul	MAR02	0.1	34.21
09-Aug	MAR02	0.1	35.42
14-Oct	MAR02	0.12	42.21
05-Sep	MAR02	0.15	44.56
28-Jun	NAR04	0.22	129.42
04-Aug	NAR04	0.31	161.42
04-Oct	NAR04	0.33	164.96
01-Sep	NAR04	0.34	186.36
28-Jun	NAR05	0.31	66.83
03-Aug	NAR05	0.35	76.18
05-Oct	NAR05	0.41	85.40

01-Sep	NAR05	0.55	90.47
03-Aug	NAR06	0.2	49.49
28-Jun	NAR06	0.21	62.64
03-Oct	NAR06	0.3	63.75
01-Sep	NAR06	0.46	82.96
07-Oct	PC01	0.12	86.73
30-Jun	PC01	0.14	101.36
08-Aug	PC01	0.16	100.25
28-Jun	RR01	0.17	41.99
06-Oct	RR01	0.17	53.06
05-Aug	RR01	0.23	62.55
01-Sep	RR01	0.56	70.12
07-Aug	RR02	0.36	42.47
03-Jul	RR02	0.53	76.59
01-Sep	RR02	0.56	50.06
06-Oct	RR02	0.57	63.30

Table B4: Periphyton chlorophyll *a* and ash-free dry mass values used in moose impact analysis for 14 headwater streams.

Site	Chlorophyll *a* (ug / cm2)	Ash-free dry mass (mg/cm2)
BJ02	3.2434	0.0036
FC02	5.6358	0.0027
FC03	31.4212	0.0057
FC04	4.4591	0.0032
MAR01	17.7127	0.0058
MAR02	28.3100	0.0074
GRA04	1.9956	0.0024
GRA05	2.5461	0.0024
NAR04	1.0047	0.0025
NAR05	2.5599	0.0048
NAR06	4.5865	0.0023
PC01	6.4134	0.0026
RR01	2.4360	0.0023
RR02	3.1654	0.0037

Table B5: Total abundance, EPT abundance, and Functional Feeding Groups of macroinvertebrates for 14 study sites. Fishing Cove River streams (FC02, FC03, FC04) and Margaree River streams (MAR01, MAR02) were sampled after heavy rainfall event and not used in the analysis for moose impacts on macroinvertebrate community structure.

	Total Abundance	**EPT abundance**	**% Filterers**	**% Gatherers**	**% Plecoptera**	**% Predators**	**% Scrapers**	**% Shredder**
BJ02	1476	633	8	67	25	66	10	22
PC01	379	194	4	55	37	57	10	38
GRA04	727	365	3	78	29	35	19	20
GRA05	1048	682	9	47	33	22	14	30
NAR04	1402	892	8	48	33	27	32	52
NAR05	1105	685	8	66	24	34	9	27
NAR06	1399	827	7	52	34	28	42	54
RR01	830	594	25	47	30	33	6	32
RR02	706	497	15	57	19	29	8	28
FC02	679	482	15	67	41	22	8	51
FC03	438	204	12	73	24	50	13	34
FC04	425	302	9	61	19	23	44	37
MAR01	2317	1344	7	63	20	51	6	30
MAR02	1304	488	6	71	19	65	6	23

Table B6a: Total abundance of family level macroinvertebrate taxa for 7 grassland streams used in the analysis of moose impacts on macroinvertebrate community structure.

Order	Family	GRA04	GRA05	NAR04	NAR05	NAR06	RR01	RR02
Ephemeroptera	Baetidae	7	74	36	14	81	2	22
Ephemeroptera	Ephemerellidae	97	35	88	207	48	92	131
Ephemeroptera	Leptophlebiidae	2	38	15	13	4	0	1
Plecoptera	Capniidae	24	65	60	44	46	6	0
Plecoptera	Chloroperlidae	101	50	61	0	110	33	22
Plecoptera	Leuctridae	75	215	335	160	309	174	75
Plecoptera	Nemouridae	8	14	7	54	10	30	34
Tricoptera	Hydropsychidae	17	36	60	6	14	187	63
Tricoptera	Lepidostomatidae	9	7	5	12	4	17	55
Tricoptera	Philopotamidae	6	55	51	80	75	22	44
Tricoptera	Rhyacophilidae	7	72	137	25	117	16	38
Tricoptera	Uenoidae	9	11	7	61	2	11	7
Coleoptera	Elmidae	16	3	316	16	382	0	0
Diptera	Ceratopogonidae	3	2	4	4	10	2	4
Diptera	Chironomidae	111	40	86	319	117	24	70
Diptera	Empididae	5	22	3	1	11	3	1
Diptera	Psychodidae	0	1	3	14	0	0	3
Diptera	Simuliidae	1	0	3	0	0	0	1
Diptera	Tipulidae	12	7	7	7	6	34	35
Acarina	Lumbriculidae	184	275	63	4	29	160	77
Bivalvia	Pisidiidae	9	2	5	20	1	2	6

Table B6b: Total abundance of family level macroinvertebrate taxa for 7 forested streams used in the analysis of moose impacts on macroinvertebrate community structure. Fishing Cove River streams (FC02, FC03, FC04) and Margaree River streams (MAR01, MAR02) were sampled after heavy rainfall and not used in the analysis for moose impacts on macroinvertebrate community structure.

Order	Family	BJ02	PC01	FC02	FC03	FC04	MAR01	MAR02
Ephemeroptera	Baetidae	3	0	1	16	63	48	4
Ephemeroptera	Ephemerellidae	47	1	51	2	78	262	44
Ephemeroptera	Leptophlebiidae	0	0	0	0	0	1	0
Plecoptera	Capniidae	5	6	8	4	0	32	16
Plecoptera	Chloroperlidae	99	24	15	19	21	19	23
Plecoptera	Leuctridae	254	102	51	10	23	196	160
Plecoptera	Nemouridae	7	3	206	71	25	219	52
Tricoptera	Hydropsychidae	112	13	0	1	4	137	17
Tricoptera	Lepidostomatidae	42	22	21	6	5	138	28
Tricoptera	Philopotamidae	10	2	93	44	13	2	46
Tricoptera	Rhyacophilidae	31	2	17	23	33	250	62
Tricoptera	Uenoidae	16	5	5	5	2	22	18
Coleoptera	Elmidae	0	0	1	7	75	13	0
Diptera	Ceratopogonidae	31	2	11	3	2	9	5
Diptera	Chironomidae	683	159	75	157	20	727	690
Diptera	Empididae	10	5	2	7	1	15	22
Diptera	Psychodidae	1	0	4	0	0	3	0
Diptera	Simuliidae	1	0	10	6	9	16	8
Diptera	Tipulidae	14	4	47	49	11	86	36
Acarina	Lumbriculidae	85	7	22	0	0	73	10
Bivalvia	Pisidiidae	0	5	9	1	4	14	26

Table B7: Summary table for models determining grassland effects on average daily maximum temperature, average temperature, maximum temperature, minimum temperature, and average daily range temperature for 13 headwater streams monitored July-September 2016. I show results for all models with $\Delta AIC_c < 8$; null models included.

Response	Variable	Estimate	Standard Error	t-value
Average Daily Maximum Temperature (ºC)	**Null Model**			
	Intercept	14.02	0.33	42.24
	Model 1 ~ Grassland			
	Intercept	13.53	0.45	29.74
	Grassland	0.02	0.01	1.52
Average Temperature (ºC)	**Null Model**			
	Intercept	12.56	0.24	53.42
	Model 1 ~ Grassland			
	Intercept	12.39	0.35	35.71
	Grassland	0.006	0.01	0.70
Maximum Temperature (ºC)	**Null Model**			
	Intercept	17.05	0.57	29.95
	Model 1 ~ Grassland			
	Intercept	16.30	0.80	20.40
	Grassland	0.03	0.02	1.95
Minimum Temperature (ºC)	**Null Model**			
	Intercept	7.98	0.16	51.43
	Model 1 ~ Grassland			
	Intercept	7.97	0.23	34.08
	Grassland	0.0005	0.006	0.08
Average Daily Temperature Range (ºC)	**Model 1 ~ Grassland**			
	Intercept	2.11	0.32	6.67
	Grassland	0.02	0.01	2.38
	Null Model			
	Intercept	2.66	0.26	10.27

Table B8: Summary table for models determining grassland effects on total nitrogen and conductivity in headwater streams monitored July-October 2016. I show results for all models with $\Delta AIC_c < 8$; null models included.

Response	Variable	Estimate	Standard Error	t-value
Total Nitrogen (mg/L)	**Model 2 ~ Grassland + (1|Site) + Alders**			
	Intercept	0.20	0.02	9.14
	Grassland	0.002	0.001	3.20
	Alders	0.011	0.002	6.28
	Null Model			
	Intercept	0.31	0.04	7.52
Conductivity (µS/cm)	**Model 1 ~ Grassland + (1|Site)**			
	Intercept	43.27	11.84	3.65
	Grassland	0.72	0.30	2.44
	Null Model			
	Intercept	64.94	9.57	6.78

Table B9: Summary table for models determining grassland effects on periphyton biomass measured as chlorophyll *a* and ash-free dry mass (AFDM) in 14 headwater streams. I show results for all models with $\Delta AIC_c < 8$.; null model included.

Response	Variable	Estimate	Standard Error	t-value
Chlorophyll *a* (ug/cm^2)	**Model 1 ~ Grassland**			
	Intercept	13.23	3.28	4.03
	Grassland	-0.19	0.08	-2.19
	Null Model			
	Intercept	8.25	2.68	3.01
	Model 2 ~ Grassland +Substrate Size			
	Intercept	24.46	9.13	2.68
	Grassland	-0.19	0.08	-2.25
	Substrate Size	-1.08	0.82	-1.31
	Model 3 ~ Grassland + Discharge			
	Intercept	15.86	4.93	3.22
	Grassland	-0.19	0.09	-2.14
	Discharge	-0.72	1.00	-0.73
	Model 4 ~ Grassland + Substrate Size + Discharge			
	Intercept	33.16	10.98	3.02
	Grassland	-0.19	0.08	-2.31
	Substrate Size	-1.46	0.84	-1.73
	Discharge	-1.31	0.98	-1.33
Ash-free dry mass (g/m^2)	**Null Model**			
	Intercept	0.004	0.0004	8.43
	Model 1 ~ Grassland			
	Intercept	4.30e-03	5.72e-04	7.51
	Grassland	-2.46e-05	1.55e-05	-1.58
	Model 2 ~ Grassland + Substrate Size			
	Intercept	6.47e-03	1.56e-03	4.14
	Grassland	-2.46e-05	1.48e-05	-1.17
	Substrate Size	2.10e-04	1.41e-04	-1.48
	Model 3 ~ Grassland + Discharge			
	Intercept	3.23e-03	1.19e-03	2.69
	Grassland	-1.92e-05	1.63e-05	-1.17
	Discharge	2.13e-04	2.08e-04	1.02
	Model 4 ~ Grassland + Substrate Size + Discharge			
	Intercept	5.42e-03	1.76e-03	3.08
	Grassland	-1.84e-05	1.53e-05	-1.20
	Discharge	-2.24e-04	1.38e-04	-1.62
	Substrate Size	2.40e-04	1.95e-04	0.25

Table B10: Summary table for models determining grassland effects on taxonomic composition, total abundance, EPT abundance, and functional feeding groups of macroinvertebrates in 9 headwater streams. Models are arranged from lowest to highest ΔAIC_c value; only models with a $\Delta AIC_c < 8$ are shown. Null models included.

Response	Variable	Estimate	Standard Error	z-value
Baetidae (# of individuals)	**Model 2 ~ Grassland + Discharge**			
	Intercept	-0.85	0.75	-1.13
	Grassland	0.05	0.01	3.79
	Discharge	0.46	0.13	3.61
	Model 1 ~ Grassland			
	Intercept	0.81	0.78	1.03
	Grassland	0.05	0.02	3.24
	Null Model			
	Intercept	3.27	0.43	7.48
Ephemerellidae (# of individuals)	**Model 2 ~ Grassland + Discharge**			
	Intercept	3.72	0.59	6.31
	Grassland	0.03	0.01	2.77
	Discharge	-0.16	0.13	-1.20
	Model 1 ~ Grassland			
	Intercept	3.23	0.47	6.97
	Grassland	0.02	0.01	2.26
	Null Model			
	Intercept	3.64	0.31	11.84
Capniidae (# of individuals)	**Model 1 ~ Grassland**			
	Intercept	1.86	0.66	2.77
	Grassland	0.03	0.01	2.31
	Null Model			
	Intercept	3.35	0.39	8.69
Philopotamidae (# of individuals)	**Model 2 ~ Grassland + Discharge**			
	Intercept	1.15	0.45	2.53
	Grassland	0.03	0.01	4.46
	Discharge	0.24	0.08	2.74
	Model 4 ~ Grassland + Discharge Dominant Tree Species			
	Intercept	0.62	0.76	0.82
	Grassland	0.06	0.01	3.21
	Discharge	0.32	0.09	3.62
	Factor (tree) alder	-1.23	0.69	-1.77
	Factor (tree) white birch	0.72	0.76	0.95
	Factor (tree) balsam fir	-0.63	1.00	-0.63
	Model 1 ~ Grassland			

	Intercept	1.95	0.44	4.39
	Grassland	0.04	0.01	3.86
	Model 3 ~ Grassland + Dominant Tree Species			
	Intercept	2.58	0.90	2.87
	Grassland	0.02	0.03	0.71
	Factor (tree) alder	0.36	0.90	0.41
	Factor (tree) white birch	-0.28	1.08	-0.26
	Factor (tree) balsam fir	-1.89	1.25	-1.51
	Null Model			
	Intercept	3.64	0.31	11.84
Total abundance (# of individuals)	**Model 2 ~ Grassland + Dominant Tree Species**			
	Intercept	6.90	0.29	23.29
	Grassland	-0.006	0.01	-0.93
	Factor (tree) alder	0.48	0.19	2.55
	Factor (tree) white birch	0.39	0.34	1.14
	Factor (tree) balsam fir	-0.96	0.35	-2.78
	Model 3 ~ Grassland + Dominant Tree Species + Substrate Size			
	Intercept	7.14	0.31	23.33
	Grassland	-0.003	0.007	-0.53
	Factor (tree) alder	0.43	0.18	2.39
	Factor (tree) white birch	0.52	0.33	1.54
	Factor (tree) balsam fir	-0.77	0.35	-2.19
	Substrate Size	-0.03	0.02	-1.46
	Null Model			
	Intercept	6.92	0.13	53.86
EPT Abundance (# of individuals)	**Model 2 ~ Grassland + Dominant Tree Species**			
	Intercept	6.61	0.27	24.83
	Grassland	-0.01	0.006	-1.93
	Factor (tree) alder	0.63	0.17	3.68
	Factor (tree) white birch	-0.17	0.31	-0.54
	Factor (tree) balsam fir	-1.35	0.32	-4.28

	Null Model			
	Intercept	6.39	0.13	47.99
Shredders (%)	**Model 5 ~ Grassland + Discharge + Dominant Tree Species**			
	Intercept	3.18	0.44	7.29
	Grassland	-0.01	0.008	-1.12
	Discharge	0.09	0.04	2.21
	Factor (tree) alder	0.66	0.23	2.77
	Factor (tree) white birch	-0.29	0.45	-0.64
	Factor (tree) balsam fir	0.22	0.42	0.52
	Null Model			
	Intercept	3.52	0.11	31.95
	Model 2 ~ Grassland + Discharge			
	Intercept	3.15	026	12.37
	Grassland	0.001	0.004	0.34
	Discharge	0.08	0.05	1.63
	Model 3 ~ Grassland + Dominant Tree Species			
	Intercept	3.84	0.41	9.47
	Grassland	-0.01	0.01	-1.63
	Factor (tree) alder	0.66	0.27	2.45
	Factor (tree) white birch	-0.75	0.50	-1.54
	Factor (tree) balsam fir	-0.21	0.47	-0.44
	Model 8 ~ Grassland + Discharge + Dominant Tree Species + Substrate Size			
	Intercept	3.18	0.42	7.42
	Grassland	-0.01	0.01	-0.60
	Discharge	0.11	0.05	2.13
	Factor (tree) alder	0.61	0.25	2.44
	Factor (tree) white birch	-0.13	0.54	-0.23
	Factor (tree) balsam fir	0.41	0.55	0.73
	Substrate Size	-0.02	0.04	-0.51
	Model 1 ~ Grassland			
	Intercept	3.42	0.21	16.04
	Grassland	0.002	0.005	0.49
	Model 7 ~ Grassland + Dominant Tree Species + Substrate Size			

	Intercept	3.69	0.43	8.51
	Grassland	-0.02	0.01	-1.76
	Factor (tree) alder	0.72	0.28	2.56
	Factor (tree) white birch	-0.87	0.51	-1.70
	Factor (tree) balsam fir	-0.37	0.52	-0.72
	Substrate Size	0.03	0.03	0.75
	Model 6 ~ Grassland +Discharge + Substrate Size			
	Intercept	3.28	0.46	7.20
	Grassland	0.001	0.004	0.29
	Discharge	0.09	0.05	1.67
	Substrate size	-0.01	0.04	-0.33
	Model 4 ~ Grassland Substrate Size			
	Intercept	3.36	0.51	6.66
	Grassland	0.002	0.004	0.51
	Substrate size	0.005	0.04	0.11
Grazers (%)	**Null Model**			
	Intercept	2.81	0.21	13.3
	Model 1 ~ Grassland			
	Intercept	2.31	0.39	5.80
	Grassland	0.01	0.01	1.39
	Model 2 ~ Grassland + Dominant Tree Species			
	Intercept	2.67	0.94	2.84
	Grassland	-0.003	0.02	-0.16
	Factor (tree) alder	0.55	0.60	0.91
	Factor (tree) white birch	-0.37	1.11	-0.33
	Factor (tree) balsam fir	-0.37	1.11	-0.33
Gatherers (%)	**Model 2 ~ Grassland + Discharge**			
	Intercept	4.24	0.12	36.57
	Grassland	0.001	0.001	0.30
	Discharge	-0.07	0.03	-2.50
	Null Model			
	Intercept	4.05	0.06	69.61
	Model 1 ~ Grassland			
	Intercept	4.04	0.11	35.78
	Grassland	0.0001	0.002	0.06
Filterers (%)	**Model 2 ~ Grassland + Discharge**			
	Intercept	1.38	0.39	3.53

	Grassland	0.001	0.006	0.22
	Discharge	0.22	0.07	3.08
	Null Model			
	Intercept	2.26	0.19	11.44
	Model 4 ~ Grassland + Dominant Tree Species + Discharge			
	Intercept	2.20	0.86	2.57
	Grassland	-0.01	0.02	-0.84
	Factor (tree) alder	0.20	0.44	0.45
	Factor (tree) white birch	-0.50	0.84	-0.59
	Factor (tree) balsam fir	-1.27	0.89	-1.42
	Discharge	0.17	0.08	2.32
	Model 1 ~ Grassland			
	Intercept	2.21	0.38	5.71
	Grassland	0.001	0.008	0.16
	Model 3 ~ Grassland + Dominant Tree Species			
	Intercept	3.56	0.74	4.81
	Grassland	-0.03	0.02	-1.52
	Factor (tree) alder	0.20	0.48	0.43
	Factor (tree) white birch	-1.48	0.88	-1.67
	Factor (tree) balsam fir	-2.17	0.95	-2.28
Predators (%)	**Model 1 ~ Grassland**			
	Intercept	4.03	0.10	38.47
	Grassland	-0.01	0.003	-4.82
	Model 2 ~ Grassland + Substrate Size			
	Intercept	3.70	0.28	13.12
	Grassland	-0.01	0.002	-5.18
	Substrate Size	0.03	0.02	1.27
	Null Model			
	Intercept	3.60	0.11	30.75